

# Towards a Biology of *Propleopus oscillans* (Marsupialia: Propleopinae, Hypsiprymnodontidae)

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*Propleopus oscillans* is one of the rarest and anatomically least known members of the megafauna of the Australian Pleistocene. Under current interpretations this large hypsiprymnodontid marsupial is usually considered to have been either a predatory carnivore or an omnivorous member of a largely carnivorous clade. Recent discoveries in South Australia extend our knowledge of the cranial and dental anatomy of *P. oscillans*. The post-cranial skeleton is also known from two humeri. The latter, although not directly associated with dental remains, are from a *P. oscillans*-containing deposit and fit no other species known in the deposit. They are also morphologically similar to, but much larger than, the humerus of *Hypsiprymnodon moschatus*, the Musky Rat Kangaroo, the only living representative of the Hypsiprymnodontidae.

Here we give an account of the previously undescribed material and give a fuller account of the material previously reported. The known material now consists of several mandibular rami (including two pairs), a rostrum and facial portion of a cranium (to which one of the pairs of rami belong), many separate teeth representing the complete juvenile and adult dentitions (excepting the second and third upper incisors) and two partial humeri.

On the basis of the morphology of the teeth of and, in particular on the interpretation of scanning electron micrographs of the sectorial premolars and the molars, the hypothesis that *P. oscillans* was a carnivorous kangaroo is reviewed. It is concluded that although diprotodont, *P. oscillans* was a carnivorous marsupial analogous with canids in being long-faced, but as in marsupial carnivores (Dasyuridae and Thylacinidae), the entire molar row has shearing, as well as crushing, specializations distributed along its length. Like *Thylacinus* and *Sarcophilus*, *P. oscillans* had a wide gape enabling it to exert bite force far posteriorly and a mandibular condyle at the level of the tooth row. It was probably an opportunistic feeder like the present-day arid zone long-faced carnivores (*Canis* and *Vulpes*).

Based on the humerus and its inferred musculature, we conclude that unlike kangaroos and wallabies, and despite its size (slightly smaller than the largest extant macropodiform marsupials of the genus *Macropus*), the animal was quadrupedal like *Hypsiprymnodon moschatus*. *P. oscillans* was not arboreal or fossorial and its ability to run fast was evidently less than that of *Canis* or *Thylacinus*. Similarities with the humerus of *Gulo* (wolverine) suggest that it might have had some capacity for endurance running.

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**KEYWORDS:** *Propleopus*, skull, dentition, mastication, humerus, forelimb, musculature, locomotion, lifestyle.

## INTRODUCTION

**Myth or Hypothesis?**

'The notion of predatory potoroid kangaroos was created by both Archer (1984) and Flannery (1984) on reflection of the habits of living potoroids and their possession of large, serrated shearing premolars ...' (Murray 1991, p. 1111)

'*Propleopus oscillans*, killer kangaroo, or strange, but peaceful, herbivore? These are some of the possibilities facing the scientist studying remains of the extinct Giant Rat Kangaroo. There is evidence supporting both interpretations' (Flannery 1985, p. 246).

The myths that presently surround *Propleopus*, may seem fanciful – but are they? Was *Propleopus* a 'killer kangaroo' (Flannery 1985, p. 246) or a 'marsupial cheetah counterpart' (Vickers-Rich and Rich 1993, p. 197)? Did this member of the Pleistocene megafauna survive long enough to 'gobble up any of Australia's first humans'? (Archer et al. 1991, p. 120). Or, most fancifully, could it have been 'trained as an "attack roo"' (Archer et al. 1991, p. 120).

*Propleopus oscillans* has been known for more than 100 years, yet it and its two congeneric species (*P. chillagoensis* and *P. wellingtonensis*) remain the rarest of the large mammals of the Australian Pleistocene. Of the three species, there is most material of *P. oscillans*. Nevertheless, remains of *P. oscillans* are fragmentary and anatomically limited.

As a result of recent discoveries in South Australia we now have a snout, much of the face, and two pairs of mandibles (adult and juvenile) of *P. oscillans*. All of the teeth except for the second and third upper incisors are known. We also have two partial humeri (one almost complete).

The new skeletal material (including some that has been briefly described previously) serves as the basis of the present attempt to move towards a sounder understanding of the biology of *P. oscillans*. In our efforts to clarify its possible diet and environmental niche, morphology must be the prime consideration. However, other factors, such as its ancestry, its distribution and its rarity (Archer and Flannery 1985, Flannery 1985) are also relevant.

We commence this re-examination of *P. oscillans* with a brief restatement of the lines of argument upon which rest the two currently most widely advanced hypotheses; i.e. the view that this species was a carnivore and the view that it was possibly an omnivorous member of a carnivorous clade (the Propleopinae), some other members of which were more carnivorous and others less so. Following that, we describe the new material and discuss its significance for the current hypotheses, and thereby, although admittedly dependent upon information about only a small part of its anatomy, take one step further towards developing an image of the whole animal that was *Propleopus oscillans*.

The most complete statement of the hypothesis of carnivory is by Archer and Flannery (1985). This was modified later by Wroe (1996) who expanded the omnivorous alternative.

## FOUNDATIONS OF THE CURRENT HYPOTHESES

**Heritage**

Two other species of the genus (also very rare) have been described. These, *P. chillagoensis* (Archer et al. 1978) and *P. wellingtonensis* (Archer and Flannery 1985), have been regarded as Pleistocene. *P. chillagoensis* is known only from a maxillary fragment and two isolated premolars collected from a fissure at Chillagoe Caves, N.E.



Queensland (Archer et al. 1978), and *P. wellingtonensis* from a part mandibular ramus from the Bone Cave, Wellington Caves, N.S.W. (Archer and Flannery 1985). L. Dawson (pers. comm.) considers that the Bone Cave deposit may be Pliocene. An isolated lower left premolar from Boxlea coal mine, near Bacchus Marsh, Victoria (Woodburne et al. 1985), corresponds closely with one of the *P. chillagoensis* specimens and is certainly Pliocene (probably >4.1 mya, Whitelaw 1991). It is also comparable in size with the alveolus of the premolar of *P. wellingtonensis*. Since the premolars of *P. wellingtonensis* are unknown, the Boxlea specimen cannot be assigned to either species with certainty. The premolar is much too large to be *P. oscillans*.

Further evidence that the lineage of *Propleopus* (i.e., the Propleopinae) extends back well into the Tertiary (Archer and Flannery 1985) is provided by the Pliocene genus *Jackmahoneya* (Bow River, Ride 1993; Hamilton, Flannery et al. 1992) and the middle Miocene genus *Ekaltadeta* (Riversleigh, Archer and Flannery 1985; Wroe 1996). The sister clade Hypsiprymnodontinae is represented today by the morphologically very similar (except for size) living *Hypsiprymnodon moschatus* and occurs also in the Riversleigh Miocene Gag (*H. bartholomaii*, Flannery and Archer 1987) and Camel Sputum Sites. Together the two clades form the Hypsiprymnodontidae (see Ride 1993).

Of the four genera of Hypsiprymnodontidae, the living *H. moschatus* is the smallest species, weighing 0.36 to 0.68 kg when adult (Dennis and Johnson 1995). Unlike Potoroidae and all Macropodidae it does not have a sacculated stomach necessary for foregut fermentation (see Freudenberger et al. 1989). Its diet consists of high-energy foods such as insects, fruit, nuts, etc.

Proportional differences in the premolar-molar row of the two other *Propleopus* species indicate that there was some dietary diversity in the genus (Wroe 1996, Ride 1993). Further comparisons between the different *Propleopus* species are not made in this study.

If it can be assumed that *H. moschatus* is archetypal of the Hypsiprymnodontidae and that the other members of the family, in retaining a hypsiprymnodontine dentition, would have also retained its unspecialized gut, this would be an argument in favour of the hypothesis of carnivorous (or at least non-herbivorous) habits in the other members. But it is commonly held that all macropodiforms were derived from an *Hypsiprymnodon*-like ancestor. If this is so, there can be no logical reason why larger Hypsiprymnodontidae could not also have become foregut fermenters, but see Ride (1993) for a view that *Hypsiprymnodon* and the other genera of the Hypsiprymnodontidae may not be macropodiforms.

Thus, while it is plausible to attribute the dietary requirements of *H. moschatus* for high-energy foods (including animal protein) to *P. oscillans*, the argument if based on relationships alone cannot be regarded as more than suggestive.

## Rarity

*P. oscillans* is a rare fossil. Most occurrences are of fragments of single individuals. In all less than 30 individuals are known. While it is characteristic of predator numbers that they are low compared with prey species, it is not the only factor that results in rarity in the fossil record, even in the case of Quaternary fossils where most species are abundantly represented. For instance *Palorchestes*, certainly a herbivore, and the termite-eating *Tachyglossus* are even rarer than *P. oscillans*, while the Tasmanian Devil (*Sarcophilus*) is not uncommon, although nowhere nearly as common as kangaroos. This evidence suggests that *P. oscillans* was solitary but, while its rarity is not inconsistent with it being a predator, many other reasons could account for the lack of fossils.

### Distribution and inferred palaeoecology

Of the seven deposits that have yielded *P. oscillans* only three are dated: Lancefield Swamp near Melbourne (26 ka = 26,000 years BP), Lake Menindee, NSW (26 ka – 18 ka), and Henschke's Fossil cave (40 ka – 32 ka). Pollen at Lancefield indicates a treeless



Figure 1. Localities at which *Propleopus oscillans* has been collected.

savannah and a colder and drier climate than at present but there is some doubt about the relevance of the date to the fossils and it is possible that the deposit is secondarily derived and hence that the pollen data do not apply to the *P. oscillans* remains (Van Huet 1994a, 1994b; White and Flannery 1995). There can be no doubt that Menindee between 26 ka and the glacial maximum at 18 ka was arid (but there is doubt that the date of the deposit applies also to the faunal remains, Balme and Hope 1990). Other mammals in both faunas were grazers and browsers (for faunal lists and dates of the deposits see Gillespie et al. 1978; Tedford 1967). The browsers, such as the *Sthenurus* species of kan-

garoos, presumably browsed on such shrubs as *Chenopodiaceae* (salt-bush, bluebush) and low trees (Wells and Tedford 1995). The fauna of the Henschke's Fossil Cave deposit (Pledge 1990) indicates a well watered but semi-arid savannah environment, possibly swamps, with open sclerophyll forest and heaths.

In all deposits from which *P. oscillans* has been recovered, grazing and browsing *Macropodidae* are common. From this it is clear that a major high-energy resource present in the original environment would have been the tissue of herbivorous mammals. However, other high energy food sources, such as birds, reptiles, arthropods, fruits, roots, nuts and seeds, would also have been present (e.g. in the same way in which arid and semi-arid Australia provided sufficient resources to sustain Aboriginal populations). The question as to whether various plant foods could have made a significant contribution to the sustenance of an animal the size of *P. oscillans*, depends upon their abundance and the species' ability to harvest them. Thus, taken by itself and without consideration of masticatory morphology, the occurrence of *P. oscillans* in the arid zone during the maximum aridity of the late Pleistocene, provides only equivocal support for a hypothesis of carnivory.

## Morphology

Prior to the discovery of Henschke's Fossil Cave near Naracoorte, South Australia, the morphology of *Propleopus oscillans* was known only from a partial adult mandibular ramus with its teeth, the holotype (De Vis 1888; see Woods 1960, fig. 1, and Archer and Flannery 1985, fig. 3.1), a portion of a left ramus with P3-M3 (Tedford 1955, 1967; figd Archer and Flannery 1985, fig. 3.3); a lower incisor (Woods 1960), two premolars, a molar and a number of dental fragments (Tedford 1967; Gillespie et al. 1978), and a maxillary fragment with a contained premolar and two molars (Bartholomai 1972, pl. 8). All were from sites believed to be Pleistocene (eastern Darling Downs, southern Queensland; Menindee, western New South Wales; Lancefield, southern Victoria) (Fig. 1).

From this material, Archer and Flannery (1985, p. 1346) pointed to the stout lower incisors with a ventral enamel border, wearing to a sharp anterior edge and the ridged, cusped, non-slip premolars as features that can be interpreted as adaptations to carnivory. Large ridged premolars in smaller animals (*H. moschatus*, *Bettongia*, and *Burrhamys*) are used to 'slice insect integument and plant matter (i.e., seed coat)'. They also drew attention to the possession of a notch between the premolars and molars that could have functioned in much the same way as the carnassial notch in *Carnivora*, and to low crowned molars unsuited to grazing, coupled with the possession of prominent molar cingula that in other mammals function to protect the gums from splinters. In addition Archer and Flannery reported that scanning electron micrographs that they had taken of an upper premolar showed very coarse wear striae which were larger than those present on the premolars of most carnivores and approached only in size by those of *Thylacoleo carnifex* examined by Wells et al. (1982). They advanced their conclusions as follows:

'In summary, the giant rat kangaroos show many dental similarities with much smaller omnivores/insectivores. Where they differ, the specializations present in the species of *Propleopus* can be interpreted as adaptations to carnivory' (Archer and Flannery 1985, p. 1347)

Then, taking into account the apparent reduction in molar row, and premolar hypertrophy, in *P. chillagoensis*, they suggested of *Propleopus oscillans*, that:

'...its retention of a large molar area and smaller premolars may indicate that it was more omnivorous, perhaps taking a range of food similar to that taken



by baboons in Africa today.' (Archer and Flannery 1985, p. 1347)

Subsequently, Wroe, as a result of a study of the species of *Ekaltadeta*, as well as *Propleopus*, brought together the hypotheses of omnivory and carnivory to conclude that within the clade of Propleopinae, extending back into *Ekaltadeta*, there may be 'two extremes of propleopine adaptation. *Propleopus oscillans* with premolar hypotrophy' (i.e. relatively reduced premolars) 'and an extended molar battery possibly included more plant material in its diet' while the other lineage 'with a reduced molar array and premolar hypertrophy appears better adapted for a carnivorous niche' (Wroe 1996 p. 689).

#### MATERIAL OF *P. OSCILLANS* STUDIED<sup>1</sup>

Henschke's Fossil Cave was discovered in 1969 and between 1969 and 1981 numerous specimens of *P. oscillans* were recovered by the South Australian Museum (Pledge 1981, 1990). The excavation was extended by John and Julie Barrie and their associates (Barrie 1990). The first collection of separate teeth of *P. oscillans* from Henschke's Fossil Cave were described by Pledge (1981). He suggested that a humerus from the same deposit was also of *P. oscillans*. Here we report additional discoveries from the same deposit. These specimens consist of the rostral portion of a juvenile skull from the premaxilla to the orbit and zygomatic arch, and an almost complete mandible found separately, but undoubtedly of the same individual and a partial humerus. There are also a large number of separate teeth (additional to those reported previously by Pledge 1981). Except for the second and third upper incisors and the lower canine<sup>2</sup>, the specimens from Henschke's Fossil Cave represent the complete juvenile and adult dentitions. Coincident with these discoveries, an almost complete adult mandible was recovered by R.T. Wells and colleagues from the Green Waterhole at Tantanoola, S.A. (containing, as well as the other teeth, the lower canine not found at Henschke's Fossil Cave), and a fragment of a ramus and a number of molars at Hookina Creek to the west of the Flinders Ranges (Williams 1980 p.105). The material from the Naracoorte localities, together with the holotype mandible and a partial maxilla, both from the Darling Downs (Table 1), provide the basis for the present study.

Pledge (1981) tentatively identified the first of the humeri as that of *P. oscillans* on the basis of its similarities to the equivalent bone in *Hypsiprymnodon moschatus*. A fuller description and analysis of this bone is presented below along with a brief account of a second less complete humerus collected by the Barries. The post-cranial anatomy of members of the genus *Propleopus* is otherwise entirely unknown. Reconstructions of the entire animal (Knight in Flannery 1985, Schouten in Archer 1987) seem to be based on analogy with potoroids, to which *Propleopus*, as a "rat kangaroo", was thought to be most closely related.

TABLE 1

Mandibular and dental measurements of *P. oscillans* specimens.  
All in mm. l = length, aw = anterior width, pw = posterior width.

**a. Mandible:**

	Tip of $l_1$ to condyle	$P_3$ - $M_4$	$P_3$ -condyle crest of $P_3$	Depth at crest of $P_2$	Depth at	$P_2$ -condyle
P20815	175.8	57.5	119.2	42.6	-	-
P35633	c. 147.5	-	-	-	32.6	101.8

**b. Premolars:**

	$P_2$ length	$P_2$ breadth	$P_3$ length	$P_3$ breadth	$P_2$ length	$P_2$ breadth	$P_3$ length	$P_3$ breadth
P35633	9.4	7.9	-	-	-	-	-	-
P20815	-	-	14.5	9.9	-	-	-	-
P35632	-	-	-	-	8.6	8.3	-	-
F6675	-	-	-	-	-	-	15.6	11.4

**c. Lower molariform teeth:**

	Specimen No.									
	P35633	P35641	P34153	P34155	P22814	P34152	P22813	P35644	P35647	P22735
$dp_3$ l	7.6	7.9	-	-	-	-	-	-	-	-
pw	6.7	6.2	-	-	-	-	-	-	-	-
$M_1$ l	9.9	-	10.6	-	-	-	-	-	-	-
aw	8.5	-	9.0	-	-	-	-	-	-	-
$M_2$ l	11.1	-	-	11.8	10.8	11.4	11.1	11.1	-	-
aw	9.6	-	-	9.5	8.6	9.6	9.1	9.8	-	-
$M_3$ l	-	-	-	-	-	-	-	-	10.6	-
aw	-	-	-	-	-	-	-	-	-	-
$M_4$ l	-	-	-	-	-	-	-	-	-	10.8
aw	-	-	-	-	-	-	-	-	-	-

**d. Upper molariform teeth:**

	Specimen No.											
	P35632	P22736	P22734	P35642	P22815	P18541	P24678	P22826	P34151	P35645	P35646	P24681
dp <sup>3</sup> l	8.2	8.0	-	-	-	-	-	-	-	-	-	-
pw	7.8	-	-	-	-	-	-	-	-	-	-	-
M <sup>1</sup> l	10.3	-	10.0	10.0	-	-	-	-	-	-	-	-
aw	10.6	-	-	9.1	-	-	-	-	-	-	-	-
M <sup>2</sup> l	11.8	-	-	-	11.9	11.3	11.2	-	-	-	-	-
aw	10.5	-	-	-	10.2	9.7	9.9	-	-	-	-	-
M <sup>3</sup> l	-	-	-	-	-	-	-	10.6	9.8	10.6	11.5	-
aw	-	-	-	-	-	-	-	-	-	9.4	9.5	-
M <sup>4</sup> l	-	-	-	-	-	-	-	-	-	-	11.0	-
aw	-	-	-	-	-	-	-	-	-	-	7.9	-

***Propleopus oscillans* (De Vis 1888)**

*Triclis oscillans* De Vis 1888, *Proceedings of the Linnean Society of New South Wales* (2)3: 5-8, pl. 1. Combined with *Propleopus* Longman 1924, nom. nov. to replace *Triclis* De Vis 1888, junior homonym of *Triclis* Leow 1851 (Arthropoda) (Longman 1924, *Memoirs of the Queensland Museum* 8: 20-21).

### Skull

Qd Mus. F6675. – Portion of a left maxilla (Figs 5A, 9; figd Bartholomai 1972, p1. 8) with  $P^3$ ,  $M^1$ - $M^2$ , area of palate and portion of the maxillary root of the zygomatic arch present. Cattle Creek nth of Dalby, eastern Darling Downs, southern Queensland.

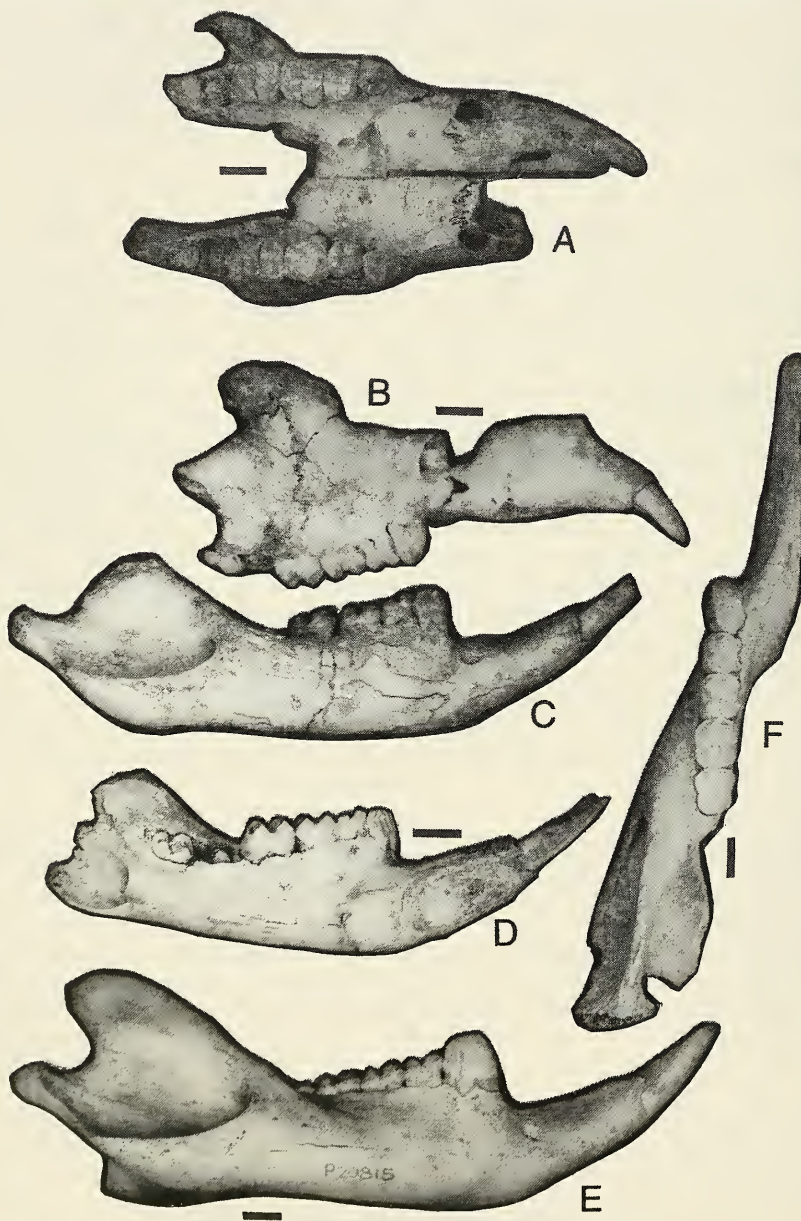


Figure 2. Skull material of *P. oscillans*. A-D: views of rostral portion of P35632 and mandible of P35633, Henschke's Fossil Cave, Naracoorte, South Australia. A: occlusal view, B: right lateral view, C: lateral view of right ramus, D: mesial view of left ramus. E-F: mandibular rami of P20815, Green Waterhole, Tantanoola, South Australia. B and C are roughly in occlusal alignment. Scale bars = 1 cm.



**P35632.** – Rostral portion of skull (Figs 2A, B; 3) consisting of incomplete right premaxilla with I<sup>1</sup> and alveoli of I<sup>2</sup> and I<sup>3</sup> and canine; right premaxillary palate complete to

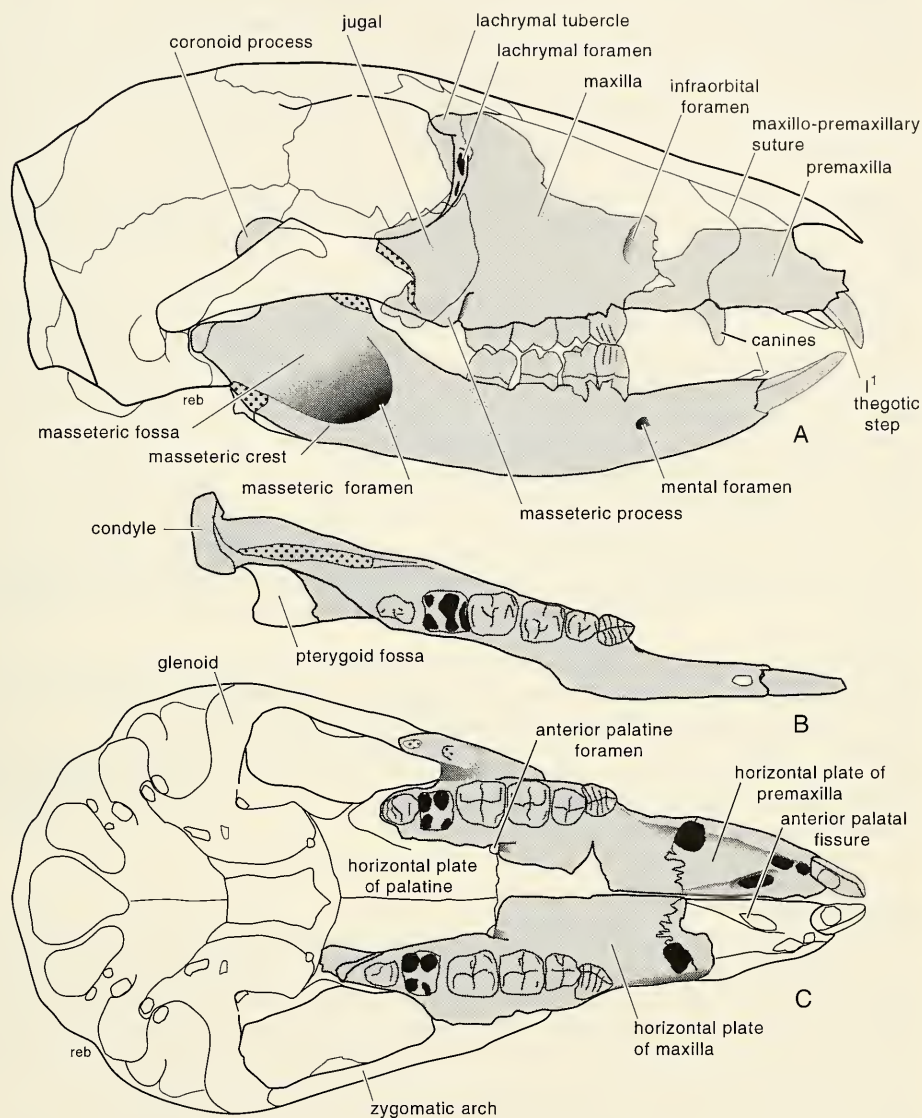


Figure 3. The Henschke's Fossil Cave specimens set within an outline of the restored skull. Terminology as used in the text. For premaxillary sutures see Fig. 19F.

median suture; left premaxilla present only as palatal fragment anterior to the maxillo-premaxillary suture; both maxillae present but incomplete; P<sup>2</sup>, dP<sup>3</sup>, M<sup>1</sup>, M<sup>2</sup>, alveolus of M<sup>3</sup>, M<sup>4</sup> erupting and exposed in crypt on both sides; posterior part of maxillary palate incomplete from immediately anterior to the palatal suture; facial portion damaged on both sides and not reaching the naso-maxillary suture; anterior edge of zygomatic arch present on right and includes the eminence representing the masseteric process; on the

right the lachrymal is present but incomplete within the orbit, its facial exposure is complete including the lachrymal tuberosity and both foramina; anterior edge of orbit present on both sides; within the left orbit a portion of the orbital plate of the palatine is present to its sutures with the jugal and lachrymal. Facial portion of maxillo-premaxillary suture present (but incomplete on left); infraorbital foramen also present (but incomplete on left); right and left portions were disarticulated along the median palatal suture when found, the right portion was fractured immediately anterior to the infraorbital foramen but the junction between the parts on both palatal and facial surfaces is in no doubt. Henschke's Quarry Fossil Cave<sup>3</sup>, Naracoorte, S.A.; Barrie locality HJD III ('high in terra rossa filling a vertical fissure between two levels' in 'upper sandy material, fossils sparse compared with lower silty deposit' - see figs 3 and 4 of Barrie 1990, vertical fissure located between i and i in section in fig. 4). Collected J. & J. Barrie and associates, Aug 1983.

P35633. - Mandible (paired rami, Fig. 2C, D) with  $I_1$ , alveolus of minute canine,  $P_2$ ,  $dP_3$ ,  $M_1$ ,  $M_2$ , alveolus of  $M_3$ ,  $M_4$  erupting and exposed in crypt in both rami; both rami broken away across pterygoid fossa; ascending rami broken across but entire condyle remains on right ramus; teeth of both rami occlude perfectly with corresponding maxillary tooth rows (P35632). Henschke's Quarry Fossil Cave, Naracoorte, S.A.; Barrie locality HJD5 ('found after excavating when sorting material in block adjacent to HJD III'). Collected J. & J. Barrie and associates, Sept 1983.

P20815. - Mandible (paired rami, Fig. 2E, F;  $P_3$ , Fig. 5B) with  $I_1$  (figd Vickers-Rich and Rich 1993, fig. 309); canine present on left side, alveolus on right,  $P_3$ - $M_4$ ; right ramus lacks only tip of incisor and small portion of pterygoid shelf lateral to the angular process; left ramus lacks angular process, posterior end of masseteric shelf, and articular surface of condyle. Collected R.T. Wells and associates, Green Waterhole, Tantanoola nr Mt Gambier, S.A.

Qd Mus. F3302. - Left ramus (figd Woods 1960, fig. 1; Archer and Flannery 1985, fig. 3-1) extending from the incisor to the anterior edge of the masseteric fossa, with  $I_1$ ,  $P_3$ ,  $M_{1-4}$ . Holotype. Kings Creek, eastern Darling Downs, southern Queensland.

P22425a. - Portion of right ramus from mental foramen to anterior edge of pterygoid fossa; roots of  $P_2$ ,  $dP_3$ ,  $M_1$  (broken posterior moiety only),  $M_2$  shattered (hypoconid lost),  $M_3$  partly erupted,  $M_4$  exposed in crypt (entoconid broken off). Hookina Creek, west of Flinders Ra., S.A.

## Separate Teeth

All separate teeth studied were collected at Henschke's Quarry Fossil Cave. Those collected by Barrie et al., were collected between 1982 and 1986 from the cave locality HJD (Barrie 1990, figs 3 and 4); those collected by S.A. Mus. party and Pledge et al. were collected between 1969 and 1981 at localities S.A.M. and HNXI in Barrie (1990) (see Pledge 1981, table 1 and fig. 1 for a section through the S.A. Mus. excavation with areas and levels from which the teeth were collected, and Pledge 1990 for a plan of a part of the areas excavated; also see Barrie, loc. cit. for the relative positions of the two excavations). Locations within the cave at which specimens were excavated are recorded here employing the notations used by Pledge and Barrie (op. cit); in the former case they are given in the form 'area/level', in the latter the area is HJD followed by a Roman numeral indicating the 'dig lot' - see Barrie (1990, p. 141).

Most of the separate teeth are no more than 'crowns' (i.e., teeth in which the enamel fully invests the tooth and dentine has formed within, but roots may not be preserved) or caps (i.e., teeth consisting only of a thin skin of enamel, with or without a dentine lining); in the latter, although cusp development is complete, margins may be at various stages of development (from 'margins unformed' to 'margins almost fully formed'). In the case of crowns, there may be some degree of wear.

All separate teeth examined are in the collection of the South Australian Museum.

Incisors: I1: P35634 (left) and P35635 (right).— Pair of I<sup>1</sup>s (right tooth split, fragment of lateral portion only); freshly erupted but with slight wear. Barrie locs HJD/X and HJD/IV. P22816.— Left I<sub>1</sub>, crown (i.e., exposed portion) with root broken off well below alveolar margin, loc. A11X/14+ (see Pledge 1981, table 2 legend, for explanation of his notation), collected G. Kilsby, 6.1.80, (figd Pledge 1981, fig. 2).

Canines: C: P35636.— Right upper canine, wear commenced at tip, Barrie loc. HJD/IV.

Sectorial Premolars (P2, P3): P2: P24677.— Right P<sup>2</sup> (Fig. 5C) in fragment of maxilla, much worn, N.S. Pledge et al. 1970s, loc. data lost; P35637.— Right P<sup>2</sup> crown, roots broken away, Barrie loc. HJD/X; P35638.— Right P<sup>2</sup> crown, fragment only, Barrie loc. HJD/X. P34154.— Left P<sup>2</sup> crown (Fig. 5D), roots broken, S.A. Mus. party, loc. slumped sediment centred on area 11 (i.e., loc. A11x/14+ - see Pledge 1981, table 2 legend, for explanation of this notation), 6.1.80.

P3: P24679.— Right P<sup>3</sup> cap (unerupted, margin almost fully formed), Pledge et al. 1970s, loc data lost; P22733.— Left P<sup>3</sup> cap (unerupted, margin unformed), N.S. Pledge et al., loc A6/10, 22.6.77, (figd Pledge 1981, fig. 2, as P3, P24680.— Right P<sup>3</sup> cap (unerupted, margin not fully formed), Pledge et al. 1970s, loc. data lost; P35639.— Right P<sup>3</sup> cap (unerupted, margin not formed), loc. HJD/X; P35640.— Right P<sup>3</sup> cap (unerupted, margin not formed), loc. ?

Deciduous (Molariform) Premolars (dP3): P22736.— Right dP<sup>3</sup> (Fig. 6) cap (unerupted, margin not fully formed), Pledge et al., loc. A7/9, 23.1.77, (figd Pledge 1981, fig. 2, as rM<sup>1</sup>). P35641.— Left dP<sub>3</sub> (Fig. 6) crown, without roots, loc. HJD/X.

Molars (M1-M4): M1: P22734.— Right M<sup>1</sup> cap (unerupted), Pledge et al., loc. A7/9, 23.1.77; P35642.— Right M<sup>1</sup> (Figs 6, 20, 22) crown, roots broken away, virtually unworn, Barrie et al., loc. HJD/X; P34151.— Left M<sup>1</sup> cap (unerupted, margin not fully formed), loc. D6/1+2, excavated A. Rundall, 13.10.79; P34153.— Left M<sup>1</sup> (Figs 6, 20) cap (unerupted), Pledge et al., loc. F08, excavated J. Bernards, 17.3.79; P35643.— Left M<sub>1</sub> cap (unerupted), trigonid broken away from across crest of protocristid, Barrie loc. HJD/X.

M2: P22815.— Right M<sup>2</sup>, crown (unerupted), loc. A6/11, coll. D. Leslett (figd Pledge 1981, fig. 2, as rM<sup>3</sup> or <sup>4</sup>); P24678.— Right M<sup>2</sup>, tooth in maxillary fragment, Pledge et al. 1970s. P18541.— Left M<sup>2</sup> (Figs 6, 22) crown (unerupted), N.S. Pledge 12.10.74, loc. A3/11 [= A3/ depth 60"-66"]; P34155.— Right M<sub>2</sub> (Figs 6, 22) crown (unerupted), loc. A2/11, coll. 15.11.80; P22813.— Right M<sub>2</sub>, cap (unerupted, margin not fully formed), loc. A10/12, (figd Pledge 1981, fig. 2); P22814.— Right M<sub>2</sub>, cap (unerupted, margin not fully formed), loc. A7/11, (figd Pledge 1981, fig. 2); P35644.— Right M<sub>2</sub>, Barrie et al., loc. HJD/IV; P34152.— Left M<sub>2</sub>, coll. N.S. Pledge et al. (J. & J. Barrie) 1.3.81, loc. X1E/2.

M3: P22826.— Right M<sup>3</sup>, cap (unerupted, margin not fully formed), loc. A11x/14+ (see Pledge 1981, table 2 legend, for explanation of this notation), 6.1.80; P35645.— Right M<sup>3</sup>, cap (unerupted, margin not fully formed), Barrie et al., loc. HJD/X; P35646.— Right M<sup>3</sup> (Fig. 6) crown, roots broken away, Barrie loc. HWW (this location is not indicated in Barrie (1990, fig. 3); it lies within the then unexcavated area south of the 'pitfall' (indicated to the south-east of the area shown as S.A.M.) between the 'pitfall' and the tunnel leading to HJD/X. The location is about 6m south of the 'pitfall' - J. Barrie pers. comm.). P35647.— Right M<sub>3</sub> (Fig. 6) cap (unerupted, margin not formed), Barrie loc. HJD/X.

M4: P24681, Left M<sup>4</sup> (Fig. 6), cap (unerupted, margin not fully formed),



Pledge et al. 1970s, loc. data lost; P22735.- left  $M_4$  (Fig. 6) cap (unerupted), loc. A7/9, coll. N.S. Pledge et al., 23.1.77.

### **Humeri**

P18846. – Almost complete right humerus (Fig. 7) comprising most of the diaphysis but lacks part of the diaphyseal contribution to the head and the distal portion of the ectepicondyle. Collected L. and G. Henschke 1969, prob. from surface in vicinity of areas X1-X3 (Pledge pers. comm. 29.3.96), Henschke's Quarry Fossil Cave, Naracoorte, S.A. (figd Pledge 1981, fig. 3).

P35648. – Distal portion of right humerus (Fig. 8), lacks distal epiphysis. Collected J. and J. Barrie et al., Henschke's Quarry Fossil Cave, Naracoorte, S.A., Barrie loc. HJD/III.

## **METHODS**

### **Preparation of SEMs and SEM illustrations**

Specimens were coated with a 10 nm layer of pure gold using a Polaron E5000 sputter coating unit, and viewed in a Cambridge Instruments S360 scanning electron microscope (SEM) fitted with a high-brightness lanthanum hexaboride (LaB6) electron source. A 30  $\mu$ m diameter final aperture, a working distance of approximately 15 mm, electron beam current of 70 pA and an accelerating voltage of 20 kV were used as the standard operating conditions. SEM images were recorded on 70 mm (220) roll film and simultaneously digitised and output as 1024 by 768 pixel, 256 grey level, TIFF files using an Image-Slave/E (Meeco Pty Ltd, Sydney) slow-scan image acquisition board mounted in a 486 PC.

Selected TIFF files were placed in Adobe Photoshop® 3.0 to create photographic mosaics after some image processing adjustment. These mosaic images and other isolated SEM TIFF files were imported into Adobe Illustrator® version 6.0 to make up individual plates with lettering and accompanying figures.

### **Radiography**

Radiographs were prepared by xeroradiography in positive mode. X-ray factors were set at 100 kV and 10 mA and exposure times of 1 second (Fig. 4) and 1.5 seconds (Figs 19-31).

## **CRANIO-DENTAL MORPHOLOGY**

Cranial descriptions, except where indicated, are based on P35632; mandibular descriptions on P35633 and P20815. Since indications of the size of anatomical elements are mostly derived from a single individual, only approximate values are given in the text (for measurements of specimens see Table 1). Except where stated otherwise and defined in the text or illustrations (Figs 3, 19, 23), osteological terminology follows Wells and Tedford (1995); dental terminology follows Ride (1993) and Figs 18, 20 and 21.

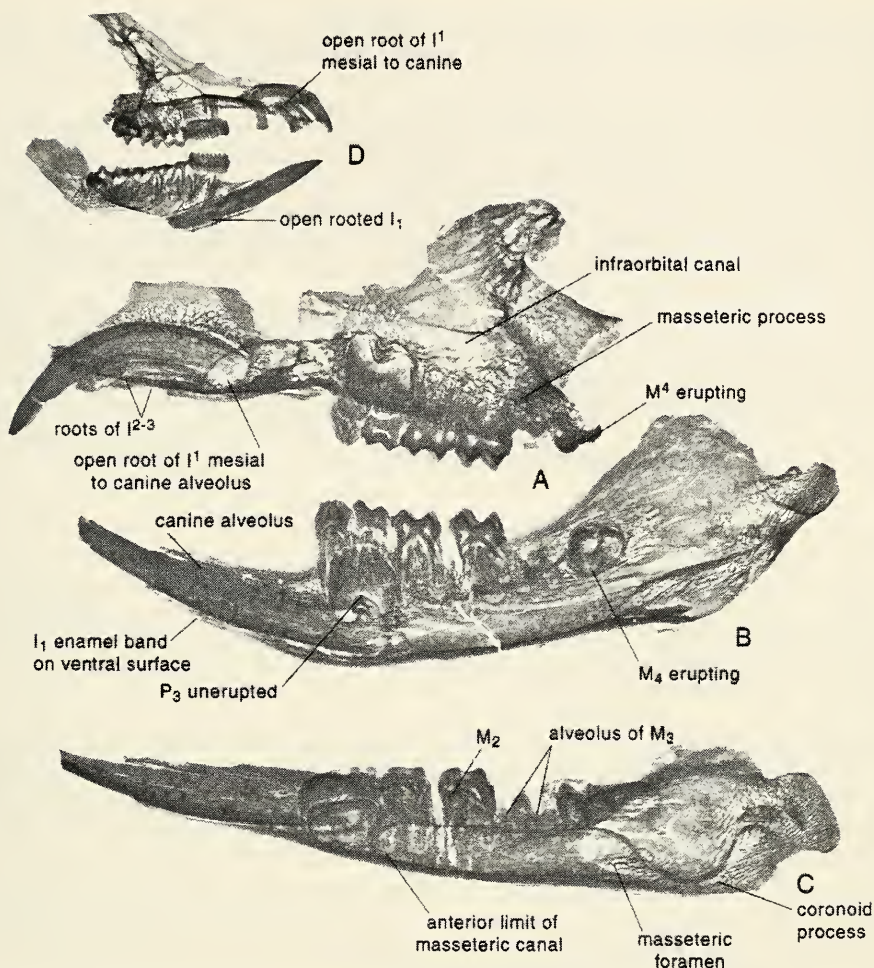


Figure 4. A, B: lateral radiographs of the cranial specimen (P35632) and left ramus (P35633) of *P. oscillans* with (D) the equivalent portions of *Aepyprymus rufescens*. C: Oblique dorso-lateral view of the mandible showing the extent of the masseteric canal. The masseteric canal is not visible in D, its dorsal surface is exposed in the fractured ventral surface of the ramus where it extends no further forwards than M<sub>2</sub>.

### Cranium (Figs 2-4)

**Premaxilla:** Ventral surface of palatal plate with distinct antero-posterior channel with edges sub-parallel with the medial suture of the palatal surface, the palatal fissure ('incisive foramen'<sup>4</sup>) lying within the channel and wholly enclosed within the premaxilla; the posterior end of the fissure is about 1/3 of the distance from the palatal maxillo-premaxillary suture to the alveolus of I<sup>1</sup>; the mesial and lateral wings of the premaxilla meet (Fig. 19) and are closely sutured postero-mesial to the fissure. The junction between them is barely visible and very close to the median interpremaxillary suture, the mesial wing continuing posteriorly as a narrow slip as far as the maxillo-premaxillary suture. The inter-premaxillary and palatal part of the maxillo-premaxillary sutures are serrate (the latter also being a scarf joint); the bone is thickened at the sutured margins. From the palatal aspect the opening of the canine alveolus lies anterior to the maxillo-premaxillary

suture, but facially the suture emerges from the alveolus about midway on the alveolar margin. The alveolus of  $I^1$  lies mesial to the canine alveolus and extends into the maxilla (Fig. 4).

**Maxilla:** On the facial surface the infraorbital foramen opens dorsal to the anterior root of the sectorial premolar and about midway between the edge of the orbit and  $I^1$ . The root of the canine lies wholly within the maxilla. The cheek teeth are positioned forward along the maxilla, all but  $M^3$  and  $M^4$  anterior to the orbit and the masseteric process of the zygomatic. The orbit, viewed dorsally, is narrow latero-mesially. The masseteric process, although broken in the specimen, was short and rounded, sutured with the jugal almost at its tip, and lay lateral to the anterior part of  $M^3$ .

The maxillary palate is entire (not fenestrated) and terminates at the level of the maxillo-palatine suture the position of which is indicated by the pair of channels of the anterior palatine foramina (which, when present in macropodiforms, are located at or close to the anterior edge of the palatines through which they pass dorso-posteriorly).

The palatal plane is virtually flat and without the flexure anterior to the maxillary tooth row as occurs in similarly-sized species of Macropodidae (Bartholomai 1973, fig. 4).

**Palatine:** Only a trace of the horizontal (palatal) plate of the palatine is preserved but the presence of the channels of the anterior palatine foramina close to the posterior edge of the maxillary palate indicates that the horizontal plate was probably unfenestrated. The orbital plate of the palatine forms the antero-mesial surface of the orbit and extends anteriorly to form the mesial margin of the large orbital opening of the infraorbital canal through the maxilla, part of which opens to the face through the infraorbital foramen (see above).

**Lachrymal:** The lachrymal bone forms the antero-dorsal margin of the orbit; the small portion remaining indicates that it was not rounded, forming a supraorbital ridge. There is a prominent lachrymal tubercle projecting from the antero-dorsal rim of the orbit. Two lachrymal ducts lie within a depression on the orbital rim. The lachrymal forms a suture with the jugal ventro-laterally immediately below the lachrymal foramina.

**Jugal:** The jugal forms the ventral rim of the orbit and constitutes virtually the entire depth of the anterior part of the zygomatic arch, extending ventrally almost to the tip of the rounded masseteric process. Sufficient of the anterior part of the zygomatic arch remains to indicate that it was not laterally bowed.

## **Mandible (Figs 2-4).**

**Dentary:** Robust. In the adult, on the lateral face, equally deep below all cheek teeth; on the mesial face, deepest below the posterior end of  $P_3$ . In the young animal, deepest below the posterior end of  $P_2$  in both surfaces. Symphysis rugose, extending the full length of the diastema and fully across the mesial surface. Genial pit well marked. Anteriorly of the genial pit the mandible inclines dorsally and the incisor is elevated above the diastema so that the incisor tips are about in the plane of the molar tooth row. Small canine present immediately posterior to the incisor alveolus. It is flattened occlusally and projects anteriorly. A small rugose area is present in the ramus anterior to  $P_3$  in the adult (P20815), but no specimens give any indication that  $P_2$  is retained after the eruption of  $P_3$  as in the related genera *Hypsiprymnodon* (Ride 1961) and *Ekaltadeta* (Archer and Flannery 1985; Wroe and Archer 1995) and probably also in *Jackmahoneya* (Ride 1993). Radiographs (Fig. 4) indicate that  $P_2$  and  $dP_3$  are replaced together by  $P_3$ .

Mandibular condyles are cylindrical, taper mesially and are transversely elongate (i.e. they are not dorsally flattened ovoids as in Macropodidae). The articular surface of



each occupies a hemicylinder extending over dorsal and posterior facing surfaces from anterodorsal to posteroventral. A line drawn at right angles to the transverse axis of each condyle lies approximately in the axis of the crest of the sectorial  $P_3$ . Mesial to the condyle, there is a prominent tubercle for the attachment of the lateral pterygoid muscle. The mandibular condyle lies approximately in the plane of the molar row (Fig. 3A) instead of being elevated well above it as in Potoroidae (e.g. *Potorous*, *Bettongia*, *Aepyprymnus*) and Macropodidae (e.g. *Macropus*, *Lagorchestes*, *Setonix*, *Protemnodon*, *Wallabia*, *Dorcopsulus* and *Dendrolagus*). It is placed lower than in other Hypsiprymnodontidae (*Ekaltadeta*, *Jackmahoneya* and *Hypsiprymnodon*).

The ascending process is wide antero-posteriorly and with a wide, rounded, coronoid process. The lateral masseteric crest of the masseteric fossa is low, raised only little above the ventral border of the mandible. Pterygoid fossa with only slightly raised rims. Masseteric fossa communicates widely antero-ventrally by the masseteric foramen into the masseteric canal. Inferior dental canal opening broadly into the masseteric canal. In radiographs (Fig. 4), the masseteric canal extends forward within the ramus to the level of the rear of the  $P_3$ .

Mental foramen for the exit of the inferior dental canal large, single, placed immediately anterior to and ventral to both  $P_2$  and  $P_3$ .

### Dentition:

**Incisors:**  $I^1$  recurved, obliquely chisel-shaped; enamel covers the anterior surface and extends part way around the sides; on the lateral side it covers about 80% of the thickness of the unworn tooth; on the mesial side it only covers about 50%. In the worn tooth (i.e., the tooth sharpened in use) there is a marked 'thegotic step' inclined across the lingual (posterior) surface where the dentine is worn away resulting in a sharp, laterally angled, chisel-like tip. The distance from the 'step' to the sharp incisive edge is about 10 mm. Radiographs (Fig. 4) indicate that the tooth is open rooted and that the anterior enamel band continues along the full length of the tooth in its alveolus. When first erupted (P35634, 5) enamel forms an apical cap which covers all surfaces, extending along the lingual surface for some 3.5 mm from the tip. Wear commences in the dentine on the posterior surface below the apical cap.

The alveolar portion of the tooth (the 'root') extends posteriorly along the full length of the premaxilla, lying mesial to and overlapping the canine alveolus and extending into the maxilla.

$I^2$  and  $I^3$  are represented only by their alveoli which slope posteriorly. From these, the teeth were small and arranged antero-posteriorly immediately behind the first beak-like pair. The antero-posterior diameters of the three incisor alveoli are: 7.7, 2.5 and 4.5 mm.

$I_1$  chisel-shaped. Enamel confined to the anterior, mesial and lateral surfaces. On the lateral surface the enamel extends about midway across the surface. Wear produces a basined, sharp, inclined, chisel edge. The tooth is open rooted and, in radiographs of both the adult P20815 and the young individual P35633 (Fig. 4), the enamel band is seen to extend the full length of the ventral surface of the tooth within the alveolus.

**Canine:** Upper canine curved and bucco-lingually compressed; lingual and buccal surfaces meet posteriorly at a ridge. Enamel on the buccal surface extending about 10 mm from the tip; on the lingual surface for about 3 mm. Lower canine<sup>2</sup> very small, located closely behind the incisor. In specimen P20815 the occlusal surface projects forward from the root and is flattened dorsally (possibly by wear).

**Premolars ( $P_2$  and  $P_3$ )**(Figs 5, 9): Sectorial, robust, anteriorly out-turned at about  $15^\circ$  to the molar row; premolars are ridged, and channelled between the ridges ('fluted').

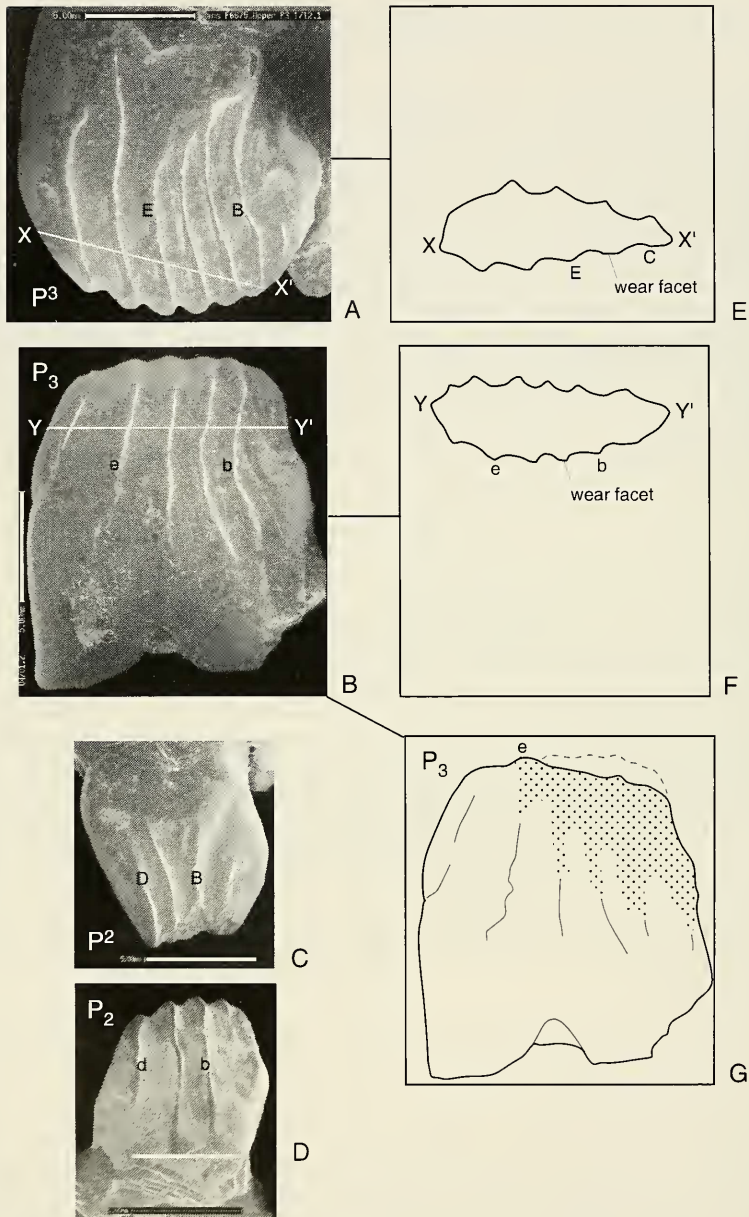


Fig 5 12/6/96

Figure 5. Sectorial premolars of *P. oscillans*: A-D, occlusal faces of A: P<sub>3</sub> (F6675), B: P<sub>3</sub> (P20815 epoxy cast), C: P<sub>2</sub> (P24677), D: P<sub>2</sub> (P34154). The crest of the P<sub>2</sub> is greatly chipped. E-F: transverse sections of casts of premolars F6675 and P20815, respectively. In each, the occlusal face is towards the lower edge of the figure. G: wear in P<sub>3</sub>; the wear facet in the worn premolar of the holotype, Qd Mus. F3302 is shown in stipple. Superimposed as a broken line is an outline of the crest of the relatively unworn premolar of P20815 to indicate the area of the tooth that becomes worn by tooth-on-tooth apposition. White scale bars in A to D = 5 mm.

Detailed descriptions of premolar surfaces and their wear features are given in the text accompanying SEM figures (Figs 10-18). In the descriptions, cusps and ridges are lettered sequentially from posterior to anterior (upper teeth **A**, **B**, **C**, etc., lower teeth **a**, **b**, **c**, etc.).

$P^3$  and  $P_3$  (Fig. 5A, B) are compressed, with cuspidate crests proud to the level of the molars (Fig. 9), and continuous along the full length of the tooth, ridged on both buccal and lingual surfaces.  $P^2$  and  $P_2$  (Fig. 5C, D) are shorter, less compressed, in plan are wedge shaped (roughly as broad as long), and with fewer ridges. Neither has a basal cingulum. Along the crest each ridge terminates in a cusp and is separated from the ridge anterior and posterior to it by a channel. Posteriorly, there is a facet for the receipt of the adjacent molariform tooth; anterior to the most anterior cusp the crest curves lingually in both upper and lower premolars.

In the maxilla Qd Mus. F6675, the tips and anterior edges of the cusps are extensively abraded<sup>5</sup> by hard inclusions within food (Fig. 10); in the mandibular cusps of P20815 abrasion grooving occurs mostly at the posterior edges of cusps (Fig. 11).

If it is assumed that planar wear can only result from attrition<sup>5</sup> produced by tooth-on-tooth contact, attrition is initially confined to facets along the hindmost ridges and in the vicinity of cusps and posterior facets, although attrition facets show abrasion as well. In both upper and lower premolars, following a narrow posterior abraded 'shoulder' of the more-or-less planar facet, the edge falls away from the ridge sharply into the succeeding channel providing an abrupt rear face to each ridge (Fig. 14). Towards the crest (Fig. 10), the descent into the channel is more gradual. Within the channels there are no planar wear facets or other evidence of tooth-on-tooth contact (Fig. 16) until adjacent ridges are obliterated by wear (Fig. 5G). Channels contain abrasion features.

The series of  $P_3$ s demonstrates several stages in the development and spread of wear facets from the unworn tooth to the worn condition. Initially, facets form anterior to the posterior edges of the hindmost ridges; in the most worn specimen (the holotype, Qd Mus. F3302, Fig. 5D), the facets in the posterior part of the tooth have widened into each other, obliterating the ridges over a wedge-shaped area extending from the tip of cusp **e** to much of the lengths of ridges **a** and **b**.

In all  $P^3$ s examined, there are 7 cusps and ridges (**A-G**). The occlusal face has the following features: The surface behind ridge **A** bears a wear facet facing slightly obliquely towards  $M^1$ . It extends to the crest where it makes a notch with the paracrista and preprotocrista of  $M^1$  which are abraded. Ridge **A** is short and extends only about 1/3 of the distance from the crest. It has only a low, rather indistinct cusp. An anterior-facing wear facet extends along the full length of the ridge and onto the extensive non-ridged and protruding area that lies between it and the enamel margin at the base of the tooth. Ridge **B** has a large anterior wear facet that is widest on the 1/3 of the ridge closest to the crest (its apical third); after that the ridge curves sharply forward to terminate close to ridge **C**.

Ridges **C**, **D**, and **E** are similar to each other. They are crescentic (convex anteriorly) and more or less parallel with each other; each has an anterior wear facet widest along its apical third. They terminate on a rounded projection (the 'lingual boss' – Fig. 18) a short distance from the enamel margin. The channels between ridges **C**, **D** and **E** come together at the boss. The ends of the channels at the boss, and the boss itself, show extensive abrasion grooves and pits.

Ridges **F** and **G** lie anterior to and do not terminate at the lingual boss; their course is almost vertical. Their cusps are extensively damaged by abrasion pitting. Wear, but not the facetting of attrition, occurs along their length and anterior on the surface anterior to ridge **G**.

All the  $P_3$ s examined have 6 ridges (**a-f**). The occlusal face has the following features: Ridge **a** is short. Posterior to it there is a postero-buccal wear surface forming a notch with an antero-buccal surface (the worn trigonid basin) of  $M_1$  bounded dorsally by the premetacristid and the protocristid. Ridge **b** traverses the full height from the crest to



the enamel margin. Leaving the crest, it curves slightly anteriorly and then posteriorly. Abrasion grooving on the wear facet is more-or-less vertical (Fig. 12). Ridges **c** and **d** are more-or-less parallel. Ridges **e** and **f** diverge from **d** basally. In the extensively worn holotype, only the cusps at **e** and **f** remain; the others are obliterated (Fig. 5G).

In all  $P^2$  examined there are 4 ridges (**A-D**). The occlusal face has the following features: Ridges **A** and **B** are more-or-less parallel (Fig. 5C, D) and before **B** reaches the enamel margin it terminates on a lingual projection smaller, but functionally similar to the boss of  $P^3$ . Ridge **C** runs parallel **D** which curves anteriorly and then posteriorly away from the leading edge of the tooth. In the very worn tooth (P24677) there is extensive chipping of the crest behind cusp **D**.

All  $P_2$ s examined have 4 ridges (**a-d**). The crest is parallel with the parametacristid of  $dP_3$  and at the same height. In occlusion with the maxillary toothrow, these two crests together match the posterior end of the crest of  $P^2$ . The occlusal face has the following features: Ridge **a** is very short terminating at a swelling where the postero-buccal margin follows the shape of  $dP_3$  which abuts it. The widest part of the tooth is at ridge **b**. Ridges **c**, **d** are parallel and diverge from ridge **b** as they depart from the crest.

Molariform teeth ( $dp_3$ , M1-M4; Figs 6, 20-22; Table 1): Both upper and lower molariform teeth are quadritubercular and rounded in outline at their enamel margins. Each has a mid-longitudinal valley which passes between the buccal and lingual cusps and is continuous from tooth to tooth, extending along the entire molar row. Although the molars are not lophodont, each is divided into three basins by transversely directed crests which fall away from near the apex of each cusp to a point of least relief at the mid-longitudinal valley. Anterior and posterior basins are only about half the length of the central basin. Since both anterior and posterior basins of each molar are only separated from the basins of the adjacent molars by very low crests, the entire molar row appears to consist of a regular series of squarish basins, contributed to by adjacent teeth. Progressing along the tooth rows, lingual and buccal marginal crests fall from the cusps into inter-molar embrasures between the teeth and, in the centre of each tooth, to a sulcus between the anterior and posterior pairs of cusps. Viewed from the lingual or buccal surface, the occluding molar rows present a margin of interlocked dentate crests.

The dental gradient is  $dp_3 < M1 < M2 < M3 > M4$ . Lower molars are only slightly narrower than the uppers.

The molariform deciduous premolars ( $dP^3$ ,  $dP_3$ ) (Fig. 6), although smaller than  $M^1$ ,  $M_1$ , are almost fully molarized, only the trigonid of  $dP_3$  being somewhat compressed where the parametacristid forms a crest continuous with the serrate crest of  $P_2$ . The last molars ( $M^4$ ,  $M_4$ ) taper posteriorly; the posterior cusps being slightly closer together than the anterior cusps and the postero-lingual cusps (metaconule and entoconid) are positioned slightly anterior to the postero-buccal cusps (metacone and hypoconid).

In the unworn upper molars (Fig. 6) there is little difference in the relative heights of the cusps. In  $M^1$ , the paracone is the tallest cusp, followed by the metacone, protocone, and metaconule; but in  $M^2$  the protocone and metaconule are taller than the buccal cusps. The remaining upper molars are only known from separate teeth of which relative cuspal heights of the implanted condition cannot be determined precisely.

Upper buccal cusps (paracone and metacone) (Figs 20, 21D, B) are more or less pyramidal with three sharp ridges, two extending antero-posteriorly (preparacrista, postparacrista; premetacrista, postmetacrista) and the other (paracrista and metacrista) transversely towards the bottom of the mid-longitudinal valley of the tooth. The antero-posterior ridges that form the centrocrista (premetacrista and postparacrista) are barely continuous across the transverse sulcus.

Upper lingual cusps (protocone and metaconule Figs 20, 21D, A, F) also have transverse ridges. But these are shorter and less pronounced than those from the paracone

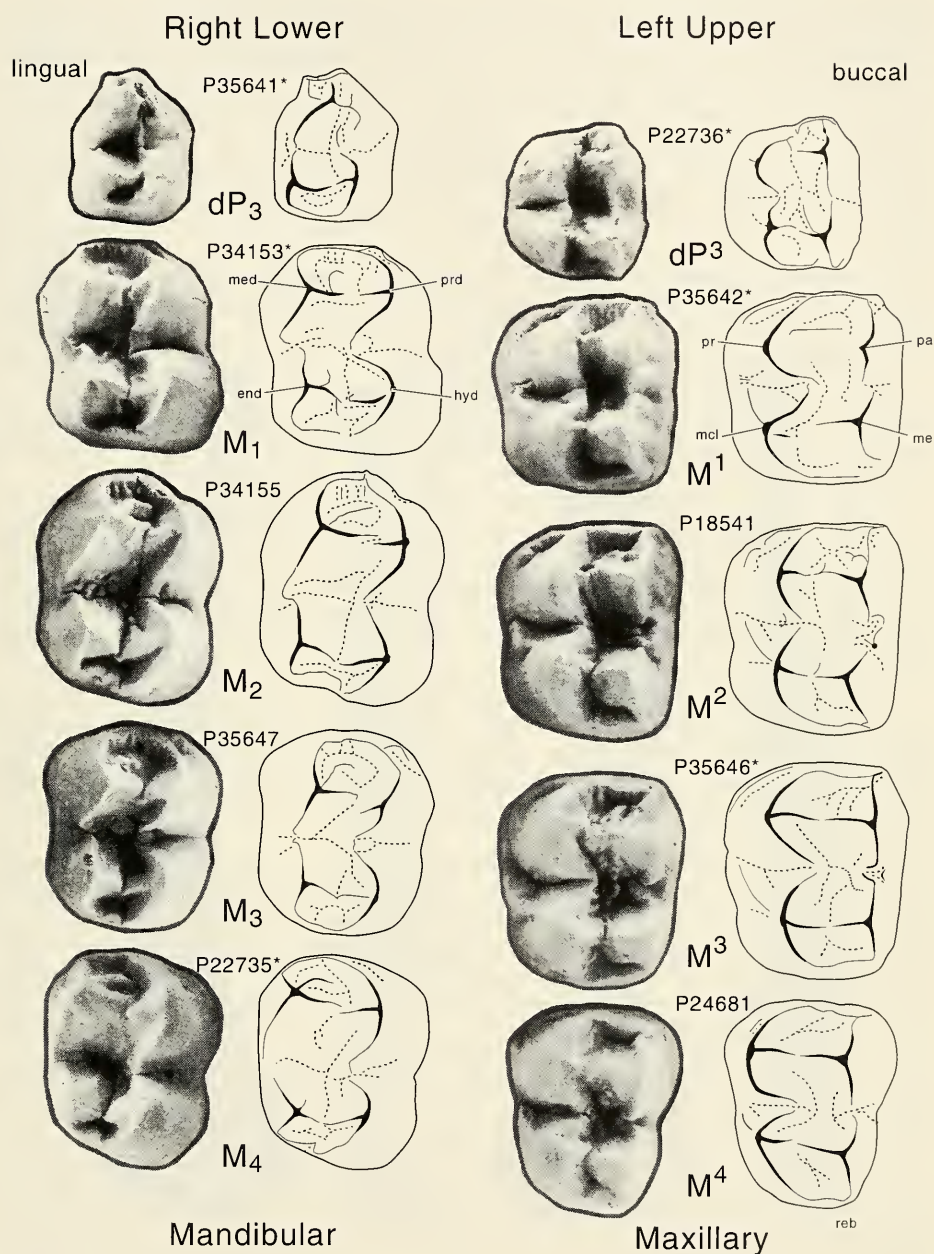


Figure 6. Unworn molarform teeth of *P. oscillans*. The teeth shown are crowns and enamel caps from Henschke's Fossil Cave (as listed in text). \*Teeth so indicated are presented as mirror images to enable comparable orientation within tooth rows. Explanatory drawings use the same conventions as in Fig. 20, in which cristae and cristids are labelled with terms used in the text. Abbreviations for the principal cusps are: uppers – pa (paracone), me (metacone), pr (protocone), mcl (metaconule); lowers – prd (protoconid), hyd (hypoconid), med (metaconid), end (entoconid).



and metacone and contribute little to the partitions across the central basin. In unworn teeth, they remain unfused in transverse ridges, their junction is marked by a fissure. The crests that run anteriorly and posteriorly from the apices of the protocone and metaconule (postprotocrista and premetaconulecrista), when unworn, follow the rounded margins of the molar with the result that lingual crests appear selenoid. Like the buccal crests, they also remain unfused across the sulcus. With wear, the tips of the lingual cusps also become low and rounded. Dentine becomes exposed at their tips (cavitation through enamel commencing at the tips of the protocone and metaconule; Fig. 21A, F). The antero-posterior ridges develop inward facing facets aligned along the mid-longitudinal valley.

The surface within the basins of both upper and lower molars (including the central basin) contains low irregular rounded projections and a few accessory spurs from surrounding crests. The parametacristid into the trigonid basin of lower molars is the most prominent of these.

On the buccal surface of upper molars only stylar cusp C is a raised stylar cusp, it is most prominent on  $M^2$  and  $M^3$  (Fig. 6). The positions of stylar cusps A and E are indicated by angular junctions of cristae at the antero-buccal and postero-buccal margins; raised cusps do not form at these points, except, possibly, in  $dP^3$  (Fig. 6).

On the lingual margins of the upper molars anterolingual cingula are present on each tooth, diminishing posteriorly along the tooth row. A metaconule accessory crista (Figs 20, 21E) slopes antero-lingually towards the lingual margin of each metaconule from near to its tip. Together the series of anterolingual cingula and the channels between the metaconule accessory cristae and the metaconules 'nest' the metaconid and entoconid as they occlude with the lingual surfaces of the protocone and metaconule (facets 4 and 5 of Fig. 21D, E; Fig. 22).

By contrast with the upper molars, in the mandible it is these lingual cusps (metaconid and entoconid) that are taller, sharper, and more acutely ridged than the buccal protoconid and hypoconid (Fig. 6). The sharper lingual cusps are more or less pyramidal with three sharp ridges, two extending obliquely antero-posteriorly (postmetacristid and preentocristid) and the other transversely (posthypocristid, entohypocristid) into the central basin of the tooth.

In the lower molars, the selenoid series of crests is on the buccal cusps (protoconid and hypoconid) (Fig. 20). The selenoid crest between the hypoconid and the protoconid probably represents the cristid obliqua. It is disjunct where its two components reach its lowest point. The buccal cusps become rounded (and ultimately, cavitated) with wear. Short transverse crests (protocristid, posthypocristid) run mesially from the buccal cusps into the mid-longitudinal valley originating somewhat mesial to the crescentic tips of the cusps. As in the upper molars, in the unworn tooth these short transverse crests do not unite with the longer transverse crests (metacristid, entohypocristid) originating from the apices of the sharp lingual cusps (metaconid and entoconid). Anterior and posterior basins have marginal crests as in the upper molars. On all lower molariform teeth a parametacristid (Ride 1993) is present; in  $dP_3$ ,  $M_1$  and  $M_2$  it originates on the transverse crest (metacristid) close to the metaconid (a raised parametaconid occurs only on  $dP_3$ ); posteriorly, in  $M_3$  and  $M_4$ , the parametacristid originates at the metaconid. Only in  $dP_3$  does it provide a functional crest continuous with the crest of  $P_2$ . In the molars it is truncated and, although running anteriorly into the trigonid basin, it terminates before reaching the paracristid.

Viewed from the rear, the mandibular toothrow twists clockwise so that the rounded buccal cusps of  $M_3$  and  $M_4$  become elevated. The mid-longitudinal valley of the molar tooth row as a whole follows in the plane of the occlusal surface of the sectorial premolar. In the most worn toothrow examined (the holotype mandibular ramus Qd Mus F3302), the rounded buccal cusps of the anterior molars wear almost to the level of the mid-longitudinal valley; in all but  $M_4$  a basin of dentine is exposed on the tips of the



buccal cusps. The Lake Menindee specimen which we have not examined personally (UCMP51697, figd by Archer and Flannery 1985, fig. 3.3) shows a more advanced state of dental wear than the holotype.

## POST-CRANIAL MORPHOLOGY

### Humeri

The humerus P18846 (Fig. 7) was briefly described by Pledge (1981). As it is the more complete of the two humeri, it is considered first here.

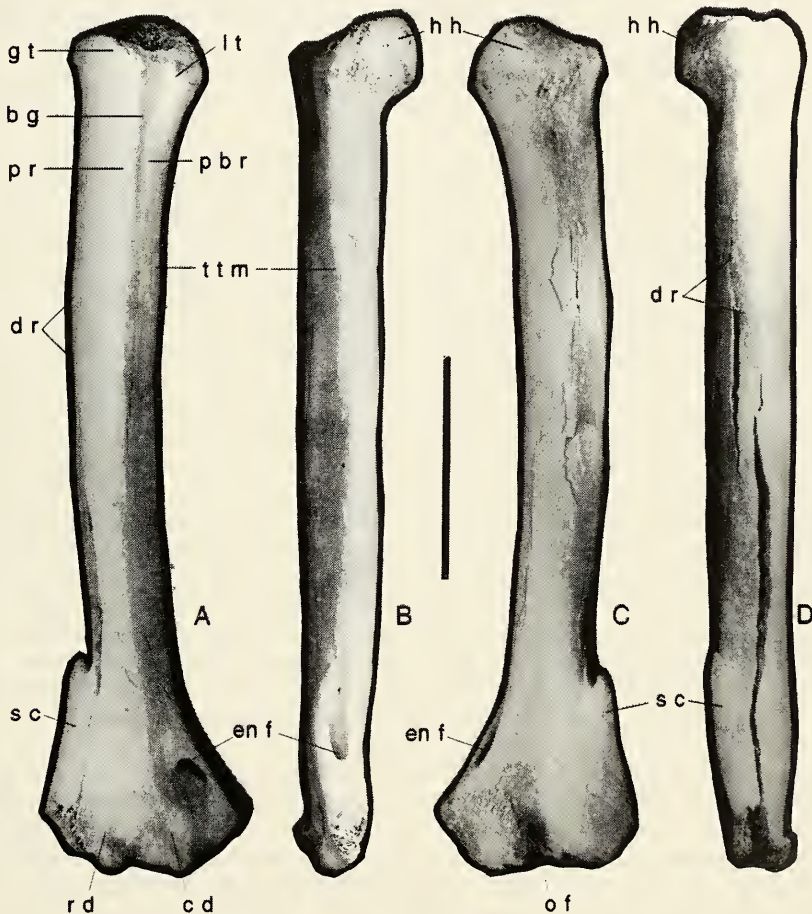


Figure 7. Right humerus (P18846) attributed to *P. oscillans*. The bone is shown in A. anterior; B. mesial; C. posterior; D. lateral view. b.g. = bicipital groove, c.d. = coronal depression, d.r. = deltoid ridge, en.f. = entepicondylar foramen, g.t. = greater (lateral) tuberosity (remnant), h.h. = humeral head (remnant), l.t. = lesser (medial) tuberosity (remnant), o.f. = olecranon (anconeal) fossa, p.b.r. = posterior bicipital ridge, p.r. = pectoral (anterior bicipital) ridge, r.d. = radial depression, s.c. = supinator (supracondylar, ectocondylar) crest, t.t.m. = tubercle for insertion of *m. teres major*. The specimen has been whitened with ammonium chloride. Scale bar = 5 cm.

Although the proximal and distal epiphyses of P18846 are missing, the diaphysis is largely intact. Proximally the diaphyseal contribution to the humeral head is incomplete; distally the outermost point of the ectepicondyle is broken away. The present length of the bone (195 mm) is less than in life and we estimate that the total length of the bone was originally close to 210 mm. The width of the bone is greatest distally where the maximum transverse dimension is presently 47 mm. Before the corner of the ectepicondyle was lost this measurement would have been greater by some 2 to 3 mm.

Proximally the bone bears evidence of a well developed head (Fig. 7B). This is very closely applied to the shank so that no narrowed neck region can be recognized. The diaphyseal contribution to the head is complete except for a small mesial portion and its terminal part. Despite the missing material it is evident that, relative to the rest of the humerus, the articular surface of the head would have been directed terminally and posteriorly (Fig. 7D). The proximal portions of both the greater (lateral) and lesser (medial) tuberosities are missing. The diaphyseal base of the greater tuberosity is larger than that of the lesser, but both tuberosities seem to have been well developed. A shallow and relatively broad bicipital groove separates these tuberosities anteriorly and although this becomes decreasingly distinct distally it can be traced down the bone over its proximal quarter.

The anterior surface of the main portion of the humeral shaft is incompletely divided by a low and rather indistinct pectoral (or anterior bicipital) ridge (Fig. 7A). The more proximal and sharp-edged portion of this extends from the base of the greater tuberosity and forms the lateral margin of the bicipital groove. It passes down over the first quarter of the bone before becoming indistinct. After a short gap, the distal portion of the pectoral ridge continues down the bone along the same alignment. The latter is a low flat-topped structure extending over the middle third or so of the anterior humeral surface.

A second low inconspicuous ridge arises on the lateral margin of the humerus about a quarter of the way down the shaft and extends a little over halfway down its antero-lateral surface. As it passes distally this ridge gradually curves anteriorly so that its most distal part lies on the anterior surface of the humerus. In living macropodiforms a ridge, which is generally more robustly developed, occupies the same general area of the antero-lateral surface of the humerus. In some larger forms the proximal and most lateral part of this ridge is locally modified to form a substantial laterally-directed tubercle (Fig. 25B). This tubercle is the structure which Owen (1876, p. 431) has referred to as an insertion of the 'pectoralis' in *Macropus rufus*. This entire second ridge is evidently homologous to the deltoid ridge of placental mammals. In many extant macropodiforms the distal extension of this ridge joins that of the pectoral ridge and together these form two sides of a triangular area (Fig. 25). This triangular area marks the site of insertion of the deltoid muscles in *H. moschatus* (Heighway 1939), *M. giganteus* (Hopwood 1974, fig. 15), *M. rufogriseus* (Pridmore and Ride unpub. data), and presumably in other macropodiform species where it occurs.

Anteriorly the base of the lesser tuberosity bears a broad ridge of low relief (Fig. 7A). This posterior bicipital ridge merges over a very short distance into the antero-mesial surface of the shaft so that it is only discernible as a separate entity over the proximal eighth of the shaft. Distal to this ridge and centred about a third of the way down the mesial surface of the bone is another low proximo-distally elongate ridge. Immediately posterior to this latter ridge and lying parallel to it, is a shallow elongate depression. By comparison with the condition in *Macropus giganteus* (Hopwood 1974), ridge and depression are thought to mark the area where the teres major and latissimus dorsi muscles inserted.

When viewed from the anterior or posterior (Fig. 7A, C) the shaft of the humerus is seen to be moderately curved (concave mesially). There is no sign of curvature from a lateral or medial perspective over the proximal three fifths of the shaft, although the posterior surface becomes very slightly convex about two thirds of the way down (Fig. 7B,



D). Aside from its proximal and distal expansions, the diaphysis is for most of its length relatively constant in diameter and approximately cylindrical in form. At mid-length the humeral shaft is 18.5 mm wide and has an antero-posterior thickness of 17 mm.

Much of the posterior surface of the humeral shaft is evenly convex, although over the distal third it gradually flattens and then becomes slightly concave due to the olecranon fossa. The antero-mesial and antero-lateral surfaces of the shaft are convex over their proximal third but show locally flattened or slightly concave regions about midway down the shaft. A flat triangular area occurs on the second quarter of the antero-lateral surface between the pectoral ridge and the deltoid one. A flattened and slightly convex area occupies the middle third of antero-mesial surface of the shaft between the pectoral ridge and internal border of the humerus. Distally both these surfaces of the shaft are convex, each akin in form to a longitudinally-sectioned cylinder.

The distal end of the humerus is laterally expanded and its antero-posterior thickness reduced. The extent of the lateral expansion is much less than occurs in humeri of similar length from *Macropus giganteus* whereas the antero-posterior thinning is relatively much greater in the fossil. Because of the absence of the distal epiphysis, it is impossible to determine whether the entepicondyle was weakly or strongly developed. However, the entepicondylar ridge is preserved and this is a weaker structure than the corresponding structure found on humeri of similar length from *M. giganteus*. On the other hand, the entepicondylar foramen which passes beneath this is as large in the fossil as in similar-sized specimens of *M. giganteus*.

The ectepicondyle is incomplete distally, but was clearly less developed than in similar-sized specimens of *M. giganteus*. It bears a supinator (supracondylar) crest that extends up the diaphysis from the ectepicondyle. This crest is formed by a shelf of bone that thins laterally over a short distance. It terminates proximally as a small peg-like process. The crest is much narrower in the fossil than in similar-length humeri from *M. giganteus*. The posterior surface of the distal humerus is marked by a large olecranon (or anconeal) fossa. On the anterior surface two small very shallow depressions can be identified; a radial depression which lies laterad of the slight convexity that represents the reverse surface of the olecranon fossa and a coronal depression which lies medially of this.

Humeral torsion, an angular measure of the orientation of the distal humerus relative to the proximal (see Evans and Krahle 1945 for definition), is difficult to measure in P18846 because of the absence of both epiphyses. Nevertheless, a reasonable estimate of the range within which it is likely to have fallen can be obtained using as the distal reference, a line passing mesially along the distal surface of the bone, and as the proximal one, a line passing through the most posteriorly directed part of the diaphyseal contribution to the humeral head and the proximal part of the lateral margin of the bicipital groove (i.e. the transition between this groove and the pectoral ridge). Measured in this way humeral torsion in this specimen lies between 12° and 27°. Comparison with values given by Evans and Krahle (1945) is not possible because the proximal reference line used in making this estimate is not the same as that used by them. Needless to say, it can be compared with measurements obtained from other species using these same reference lines (Table 3).

The second less complete humerus comes from an individual which was somewhat larger than the animal that provided the humerus of Fig. 7. Specimen P35648 is the distal half of a right humeral diaphysis (Fig. 8). It is abraded distally so that it lacks both the lateral margin of the supinator crest and the bridge of bone that closes the entepicondylar foramen medially. Despite its incompleteness, enough of the bone is available to establish that its anterior surface lacked a well developed pectoral ridge. Viewed from a proximal perspective this diaphysis is seen to be rounded-triangular in cross-section over its third quarter with flattened antero-medial and antero-lateral surfaces and a evenly curving posterior surface. These are features it shares with the more complete humerus and which set both apart from similar-sized specimens of *Macropus* and *Sthenurus*. To the



extent that this humerus can be compared with the more complete one, the two bones are very similar. Measurement of the shafts of the two bones at a level immediately adjacent to the proximal termination of the supinator crest indicates that P35648 is approximately 10% wider than P18846.

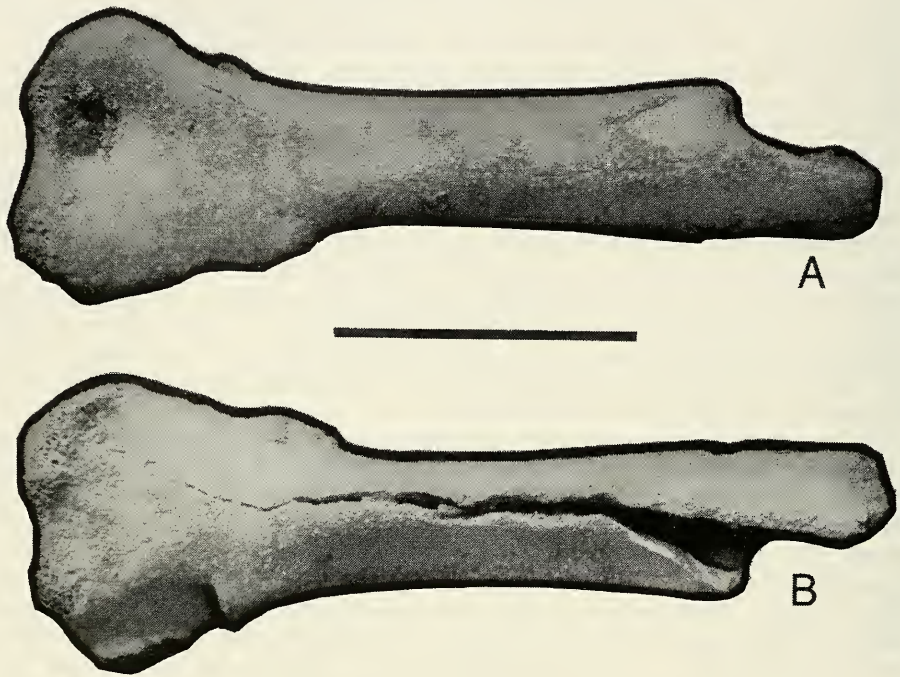


Figure 8. Additional partial humeri P35648 attributed to *P. oscillans*. The bone is shown in A. anterior view; B. posterior view. The specimen has been whitened with ammonium chloride. Scale bar = 5 cm.

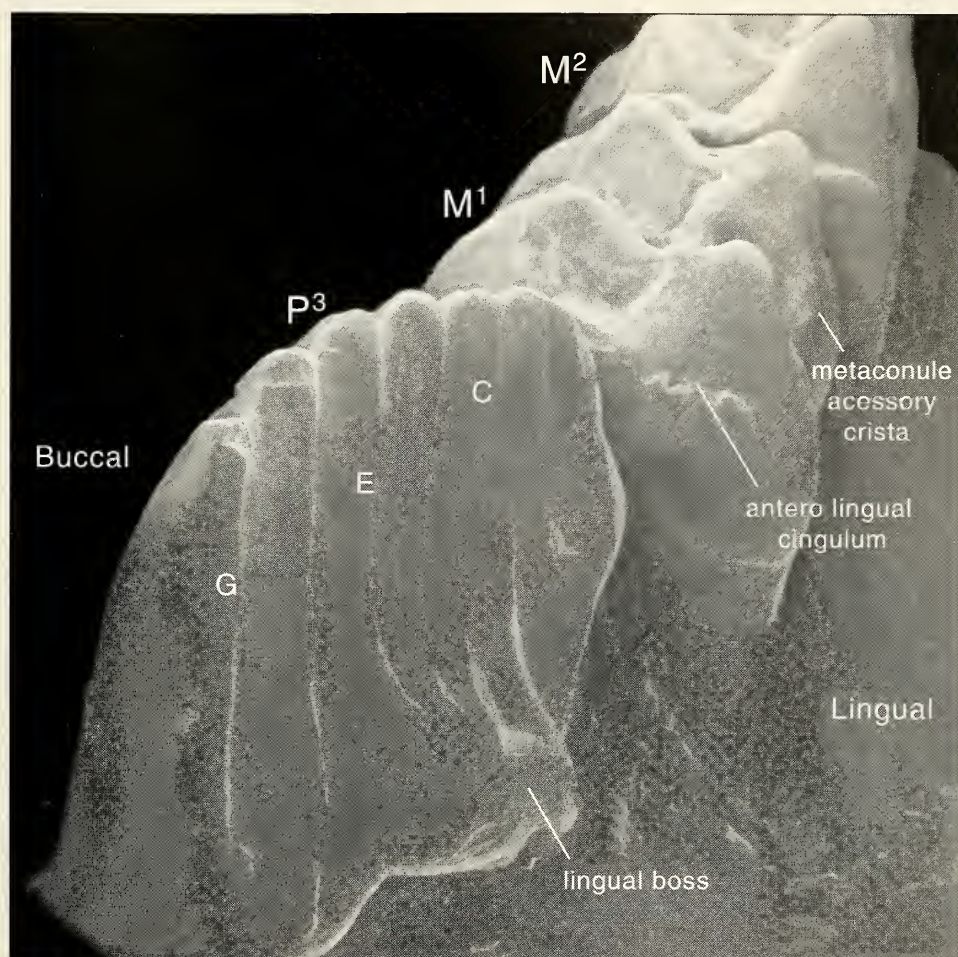


Figure 9. SEM of the left maxillary premolar P<sup>3</sup> and the anterior molars of Qd Mus. F6675, Cattle Creek, nr Dalby, Darling Downs, Queensland. The image is from the antero-mesial aspect and shows the occlusal features of the upper tooth row of *P. oscillans*.



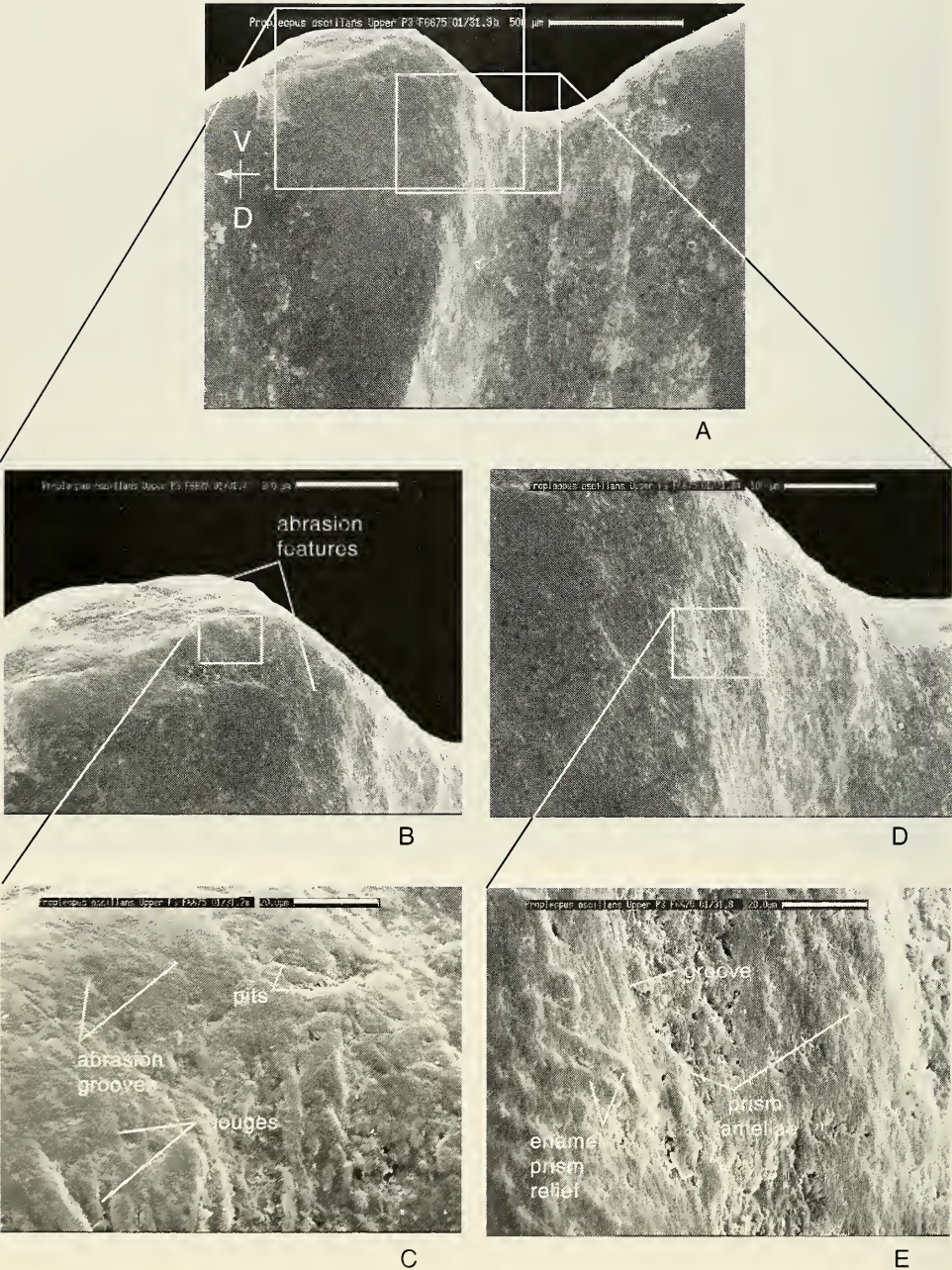




Figure 10. *P. oscillans*, P<sup>3</sup>, F6675, abrasion features of part of crest between cusps **D** and **E** viewed from the lingual (occlusal) surface. White scale bar in A = 500  $\mu$ m, B = 200  $\mu$ m, C = 20  $\mu$ m, D = 100  $\mu$ m, and E = 20  $\mu$ m.

Interpretation.- A: Cusp **E** in upper left. Wear facet **E** is the dark area on the left, wear facet **D** on the right. The paler area extending obliquely downwards from the saddle between the cusps is the commencement of the channel (**E/D**) between ridges (see Figs 15, 16). Shallow abrasion features towards the right in Fig. A (some more than 100  $\mu$ m in width) may be post-mortem artefacts caused in cleaning.

B and C: Detail of the tip and lingual surface of cusp **E** showing abrasion features – chipping on the antero-ventral face (upper left) of the tip of the cusp, pits (non-linear), gouges (short linear), and abrasion grooves (long linear). D and E: The wear surface at the commencement of the posterior edge of wear facet **E** showing prism relief exposed on the surfaces and some abrasion grooves transecting the linear patterns of prism features.

Interpretation.- Diazoal prism relief exposed on the shoulder of the ridge indicates a radial arrangement of prisms on the wear facet, a wear resistant feature; the edges of enamel lamellae appear in the channel (see Fig. 15). Chipping of the antero-ventral edge of the cusp, and pits and gouges in that area, indicates that objects may be crushed at the premolar crest, but the small amount of major damage to the cusps which are vulnerable to such fracture in both this specimen and the Green Waterhole mandible (Fig. 11) probably indicates that puncture-crushing of large hard objects at the premolar crest is not frequent. However, in much worn specimens (e.g. the holotype, Fig. 5G) and in the worn deciduous premolar (perhaps due for replacement – Fig. 5C), the cusps may be virtually chipped away. The position of this fracture relative to the cusp apex, and similar fractures on cusps **F** and **G** of this tooth, indicate that the fracturing pressure was applied to it from the mandible pressing posterodorsally. The common occurrence of small pits, gouges and abrasion grooves on the antero-lingual surface of upper cusps indicates that material subject to premolar shear frequently contained small hard inclusions.

Exposure of prism features in areas of possible tooth-tooth and tooth-food-tooth contact of mammal teeth has been interpreted as indicating fine polishing by tough but non-scratching materials (e.g. leaves, Walker, et al. 1978, fig. 3A and C), etching by dietary acids (Teaford 1988a), regurgitated stomach acids (Van Valkenburgh, Teaford and Walker 1990, pp. 325 and Pl. III), possibly tooth grinding (Teaford 1988a, fig. 1), and shown experimentally may be produced by polishing by substances softer than enamel (gas propelled NaHCO<sub>3</sub>, Boyde 1984). The concentration of exposed prism relief on certain worn surfaces in the teeth of *P. oscillans* argues against a general explanation, such as chemical etching, being the cause. It seems likely that both the exposure of prisms on the shoulders (ridges) of the wear facets, and the exposure of laminar structure along the edges and within the channels, have a common cause, namely polishing by relatively soft but tough materials. Koenigswald and Clemens (1992, p. 206) have suggested that arrangements like the prism relief observed on the ridges argue that, where the angle of prism incidence to a tooth surface is largest, as when prisms are radially arranged, wear will occur at the slowest rate, but that such surfaces are vulnerable to fracture.

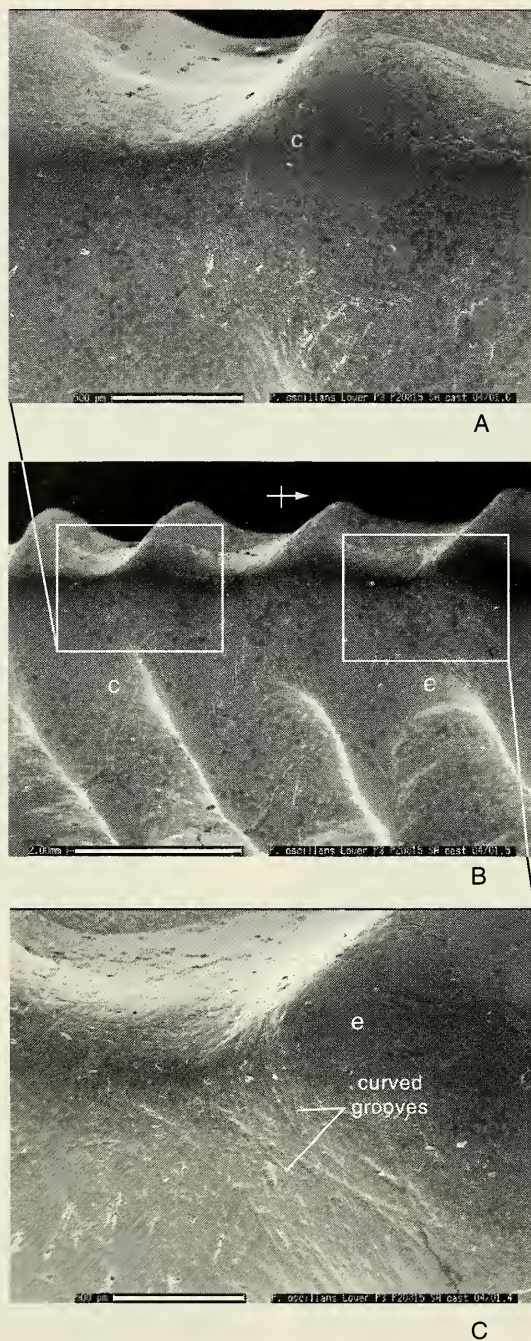


Figure 11. *P. oscillans*,  $P_3$ , (epoxy cast of P20815) abrasion features of part of crest from cusps **b** to **e** viewed obliquely from the dorso-buccal (occlusal) surface. White scale bar in A = 500 µm, B = 2 mm, and in C = 500 µm.

Interpretation.- A and C illustrate abrasion features immediately behind the cusps **c** and **e** respectively. In this specimen, although fully adult, there has been no major chipping of cusps. Pits, gouges and abrasion grooves mostly occur behind the cusps; from there, abrasion grooves run diagonally forward and ventrally onto the wear facets of the ridges beneath the cusps indicating that the cusps of the lower premolar are moved in a postero-dorsal direction.



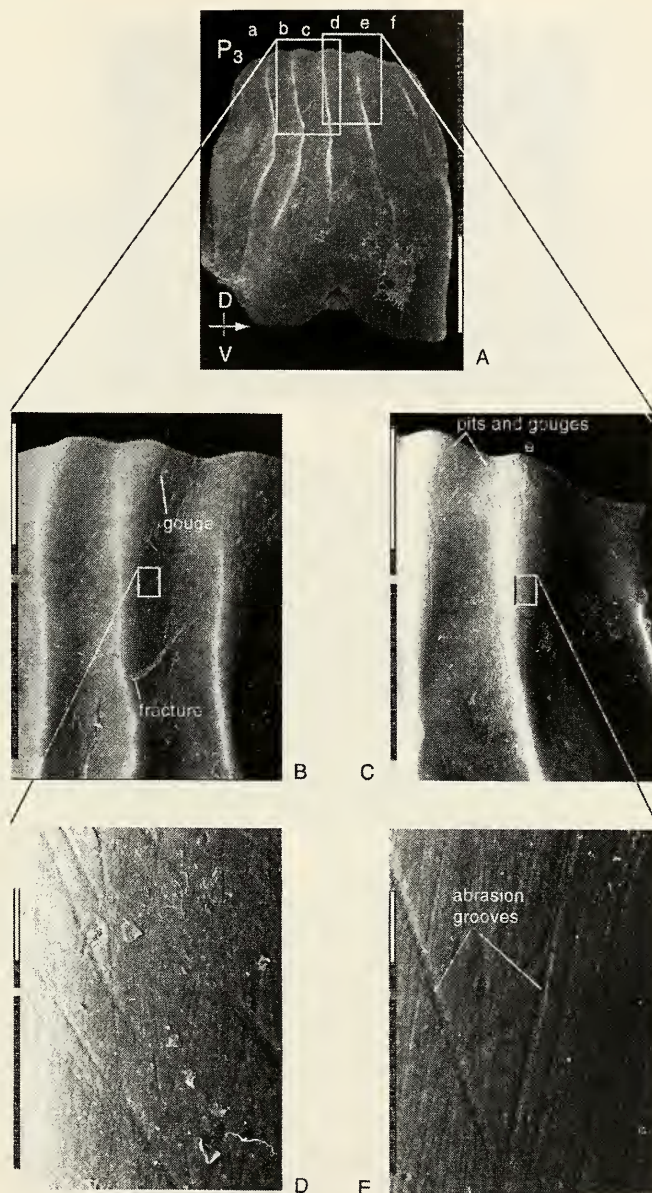


Figure 12. *P. oscillans*, P<sup>3</sup>, (epoxy cast of P20815), abrasion features of wear facets c and e. Abrasion grooves on the facets are long parallel-sided features much more regular than those in the channels (Fig. 16). White scale bar in A = 5 mm, B = 2 mm, C = 2 mm, D = 100  $\mu$ m, and E = 100  $\mu$ m.

Interpretation.- Regular grooving is typical of shearing facets of extant animals feeding on substances containing hard inclusions. Teaford (1988a, fig. 7b and d) describes it in leaf eating primates where the examples are characterized by low variation in groove width. Van Valkenburgh, Teaford and Walker (1990) illustrate it in Carnivora. There, in cheetah (pl. 1, fig. a), a flesh-eater, variation is low as compared with lion, pl. 1, fig. b) a moderate bone-eater. Feature density, as measured by the number of linear features transected by a line drawn at right angles to the general direction of the features, is comparable with lion as illustrated by Van Van Valkenburgh, Teaford and Walker (1990). In *P. oscillans*, as in the shearing facets of lower carnassials of Carnivora, there is variation in groove orientation, although the range in orientation indicates a general directional trend (more-or-less orthal). Fig. 34 illustrates comparable groove variation in the postero-lingual wear facet of P<sup>2</sup> of *P. oscillans*.



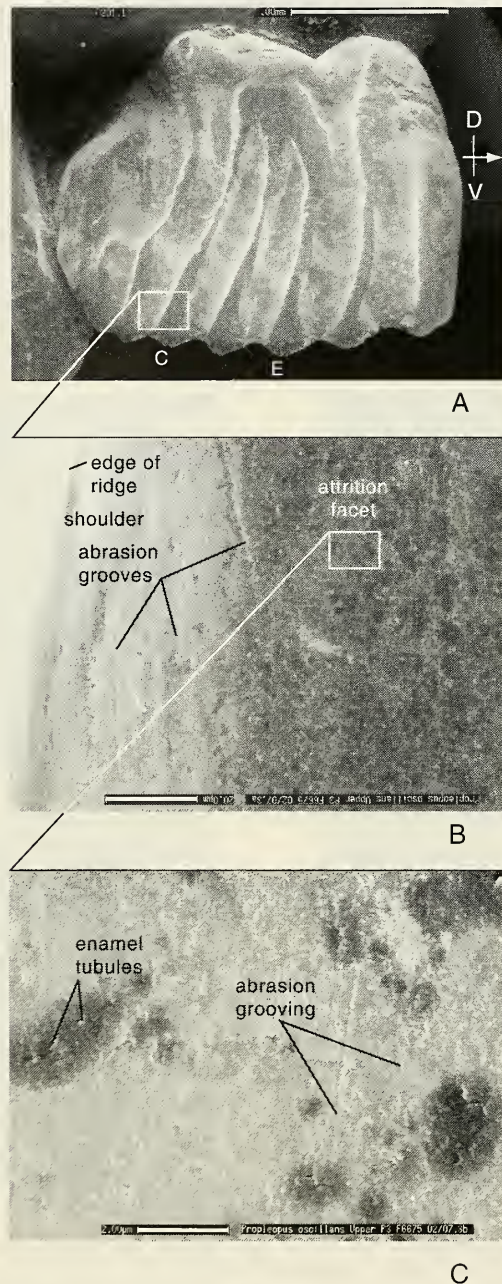


Figure 13. *P. oscillans*, P<sup>3</sup>, F6675. Abrasion features of the surface of an upper attrition facet (wear-facet C). White scale bar in A = 5 mm, B = 20 µm, and in C = 2 µm.

Interpretation.- Abrasion grooves in the surface indicate movement slightly diagonally towards the top left of the frames (posterodorsally) from the planar attrition facet across the shoulder of the ridge, and thence over the edge of the ridge into the channel. While the planar attrition surface of the facet has a polished surface without visible prism relief, the presence of clusters of openings of enamel tubules in the polished surface indicates that the area (like the shoulder, see Fig. 15) is a diazone with wear-resistant radial orientation of prisms (see Boyde and Lester 1967, for the distribution of tubules in relation to prism boundaries within marsupial enamel).

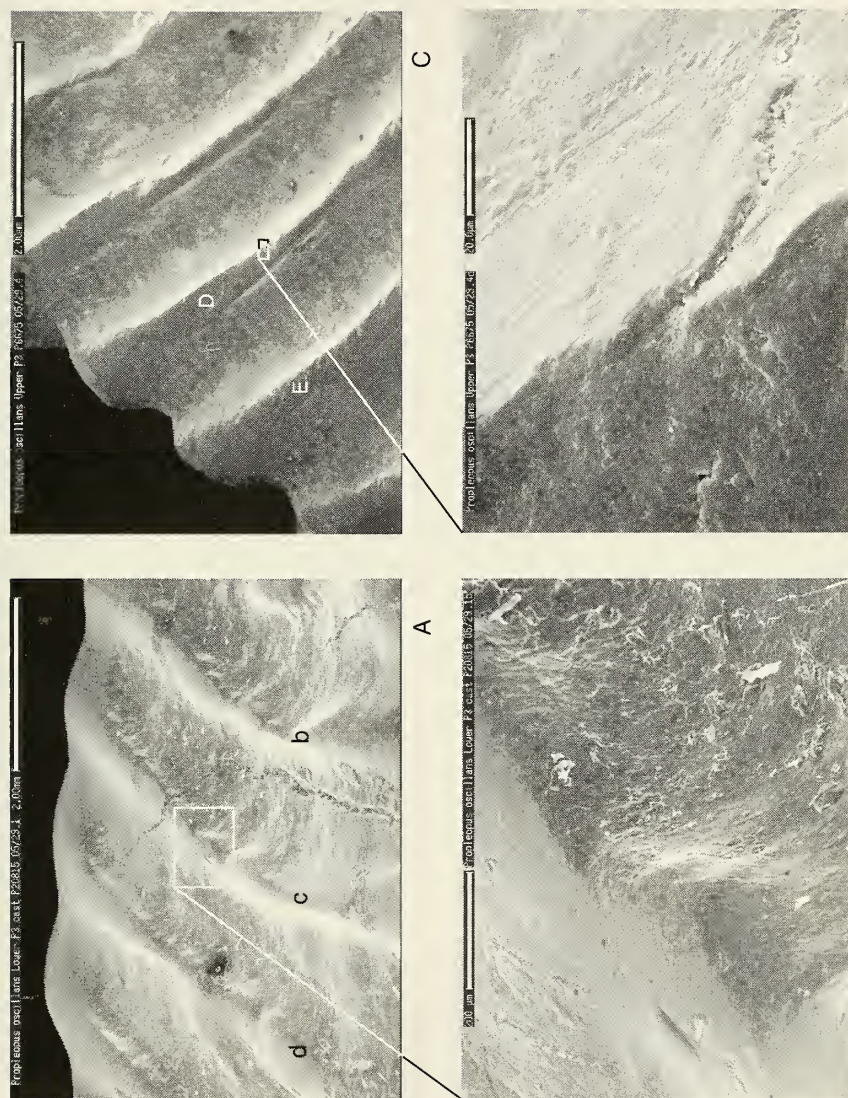


Figure 14. *P. oscillans*, A, B: P<sub>3</sub> epoxy cast of P20815 (reversed image). C, D: P<sub>3</sub>, F6675. Oblique SEM frames of the ridges and channels showing the abrupt transition between facets and their succeeding channels at the posterior edges of ridges. These face posteriorly in both upper and lower prenatals. The diamond-shaped object on the shoulder of the ridge in Fig. B (left of frame) is a casting imperfection. White scale bar in A = 200 μm, B = 200 μm, C = 2 mm, and in D = 20 μm.



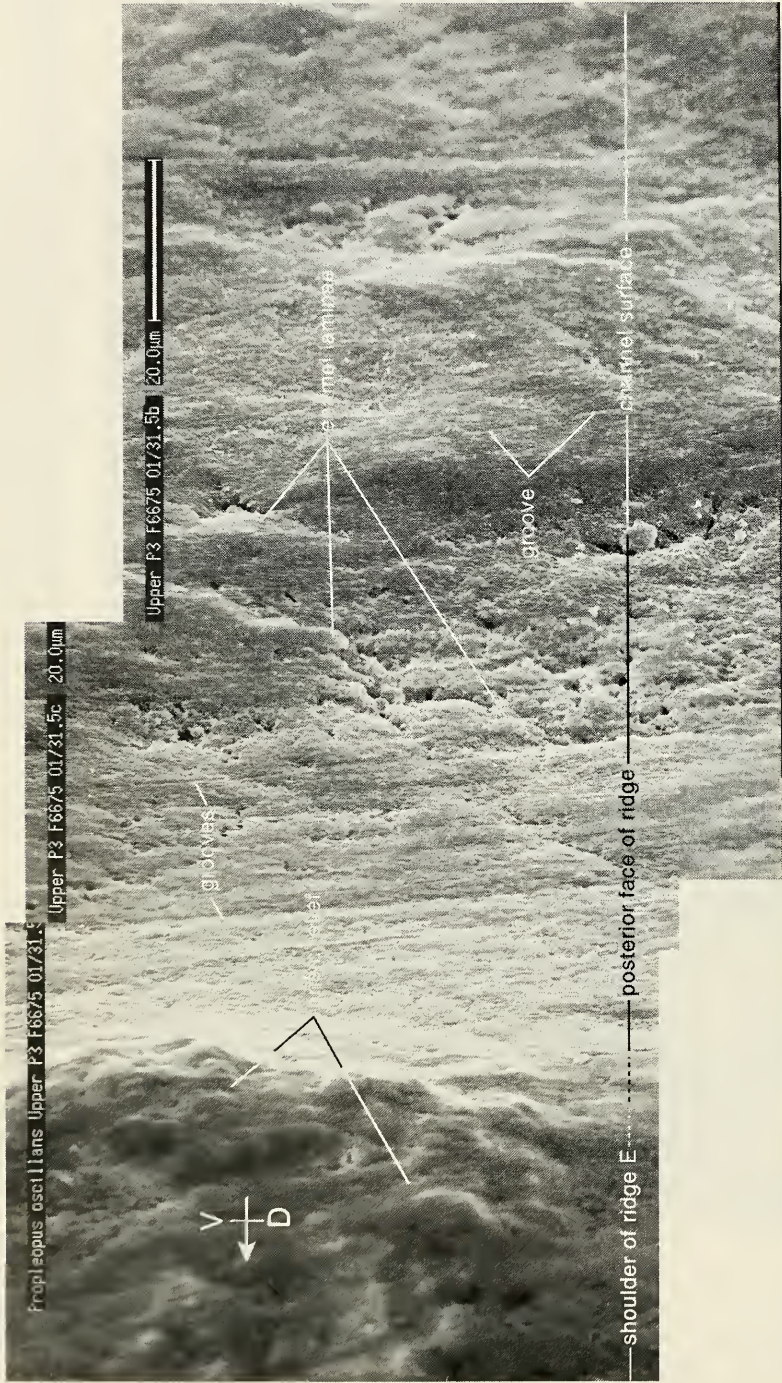


Figure 15. *P. oscillans*, P<sup>3</sup>, F6675, abrasion features of the posterior edge of ridge E on the occlusal (lingual) face. Mosaic of 3 frames from a traverse. White scale bar = 20 µm.

Interpretation:- From left to right, the dark area on the left is prism relief exposed on the shoulder of ridge E, then followed by the face of the posterior edge (see Fig. 14) with the edges of enamel laminae exposed along its length. The change from dark to light is partly due to the angle at which the electron beam strikes the edge as well as the nature of the surface; focus was maintained instrumentally during traversing, so the image appears as though it is of a flat surface. The more gently sloping surface of channel extends from the centre of the posterior edge. Long linear abrasion grooves of different widths can be observed running more or less parallel with the edge of the ridge and independent of the linearity imposed by the lamellar arrangement exposed along the edge and within the channel.

The lamellar arrangement within the channel (as distinct from the more wear-resistant radial arrangement of prisms on the ridges) reflects microstructural complexity not explained from surface detail. The detail observed may reflect an arrangement in which prisms are tangential to the surface; such arrangements are thought to be stress-resistant as distinct from wear resistant (Koenigswald and Clemens 1992). Alternatively, apparent absence of prism detail may indicate loss of prism demarcation in radial enamel towards the outer enamel surface similar to that observed in some marsupials (including the propileopine *Ekaltadeta ima*) by Gilkeson and Lester (1989); or it may indicate that the surface of the channels is aprismatic (Koenigswald and Clemens 1992, p. 199, fig. 4).



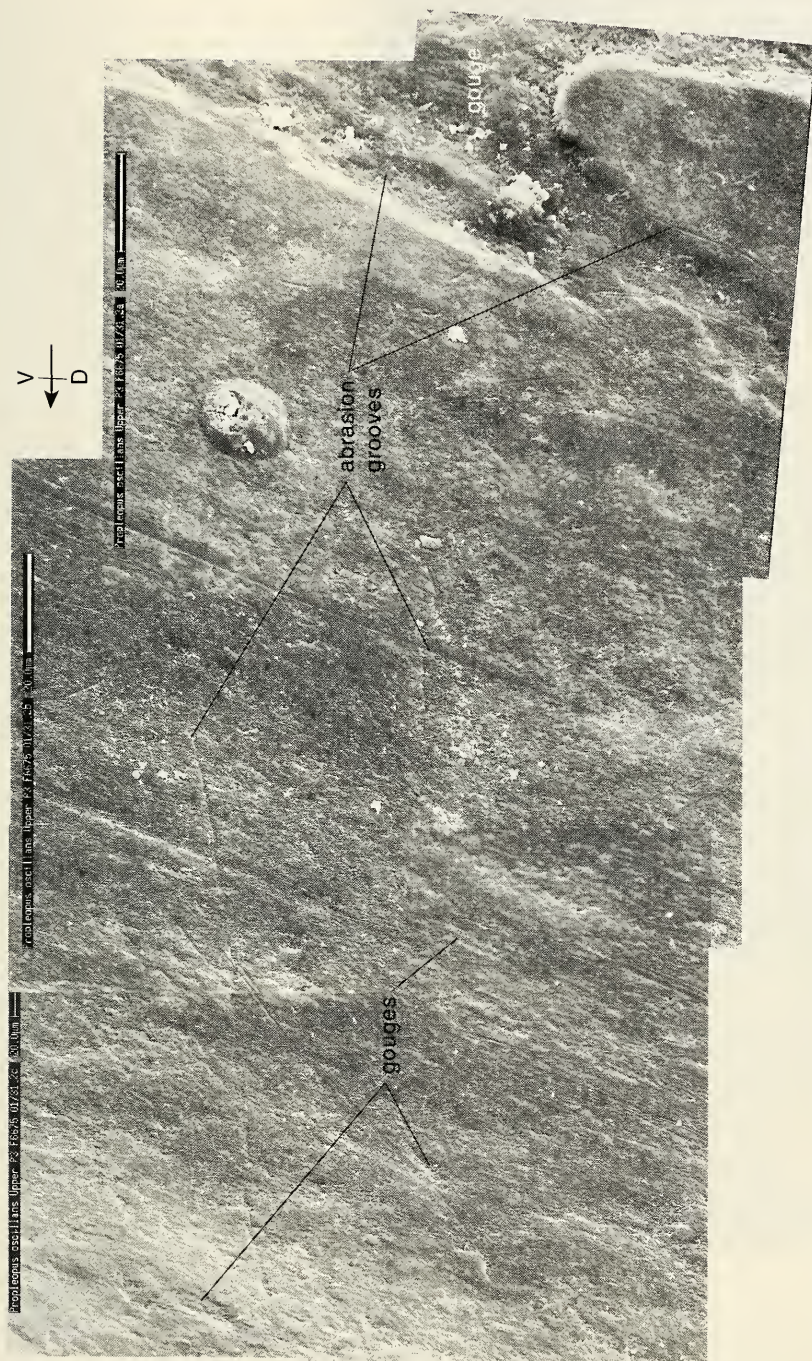


Figure 16. *P. oscillans*, P<sup>3</sup>, F6675, occlusal (lingual) face, abrasion features of the channel between ridges E and D. Mosaic of two traverses of 6 SEM frames in the plane of and posterior to the transect in Fig. 15. Long abrasion grooves running diagonally across the mosaic are approximately parallel with the posterior edge of ridge E anterior to the channel. The left of the mosaic is approximately 1/3 of the distance across the channel towards ridge D (480 µm of approx. 1420 µm). The circular object in the upper right frame is not identified. White scale bar = 20 µm.

Interpretation. - Linear abrasion features are of different widths and change in width and depth along their lengths. This probably indicates both that that incising particles vary in size and that pressure applied to them changed during incision. Large, wide but short, abrasion features (appearing like large gouges) occur. The feature in the lower right of the mosaic is the anterior edge of such a gouge (gouge approximately 50 µm in width) where a piece of enamel lamina has been removed. Grooves in this mosaic range in width from approximately 15 µm to less than 1 µm. Long parallel grooves in the centre of the mosaic are 2-3 µm across. There is no similarity between this surface and that resulting from incision by opaline phyloliths (see Walker et al. 1978, fig. 3E). Apart from the much lower feature density, the pattern of gouges and grooves (some very large) of variable width and length, and rather variable orientation, is comparable with that illustrated in the carnassials of moderate bone-eaters by Van Valkenburgh Teaford and Walker, (1990) but the carnassials of Carnivora studied by these workers showed a much higher density of features than occurs in the grooves of premolars of *P. oscillans*. However, they studied the shearing facet between the paraconid and protoconid of the lower carnassial where shearing is concentrated (as is postulated for the postero-lingual wear facet in *P. oscillans* premolars - see Fig. 34). Feature density on the ridges of *P. oscillans* is more comparable (Fig. 12) although there are few pits away from the crest.



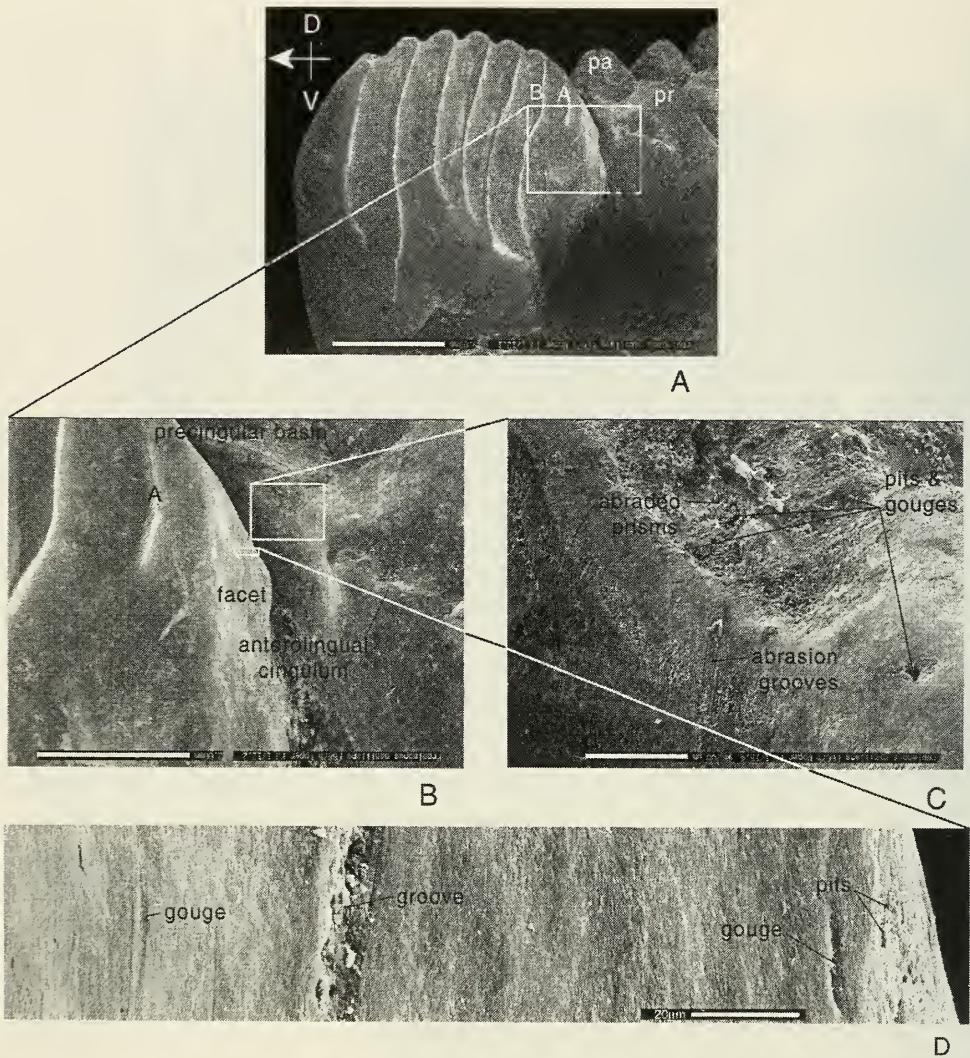


Figure 17. *P. oscillans*,  $P^3$ , F6675, abrasion features at the molar/premolar junction. A, orientation; B, wear facet and edge of ridge B, ridge A and the postero-lingual facet of  $P^3$  forming the antero-lingual face of the embrasure between  $P^3$  and  $M^1$ . Cavitation in the precingular basin antero-lingual to the protocone, and in the antero-lingual cingulum, is visible in the upper right of the frame (for terminology see Fig. 20). C and D abrasion features of the two areas indicated in B. White scale bar in A = 5 mm, B = 2 mm, C = 200  $\mu$ m, and D = 20  $\mu$ m.

Interpretation.- Cavitation and pitting in C is typical of crushing facets. Prism exposure anterior to the precingulum is similar to that illustrated by Teaford 1988b, in the interproximal facet of *Proconsul major*. D, abrasion groove and gouges in the anterior face of the embrasure between the premolar and molar also indicate that the postero-lingual facet of  $P^3$  is a shearing facet (also see Fig. 34).

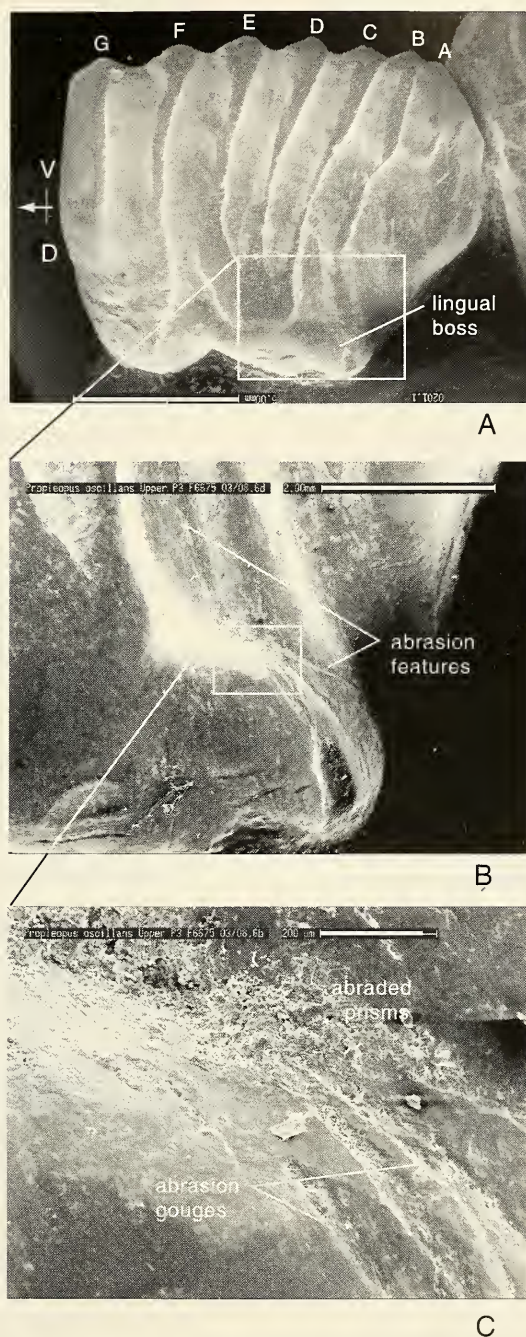


Figure 18. *P. oscillans*, P<sup>3</sup>, F6675, lingual face; abrasion features at the lingual boss. Abrasion features (including a very large gouge) are concentrated on the boss and particularly at the posterodorsal end of the channel between **D** and **C** where material forced along the channel would have been deflected from the gingival margin. White scale bar in A = 5 mm, B = 2 mm, and in C = 100  $\mu$ m.



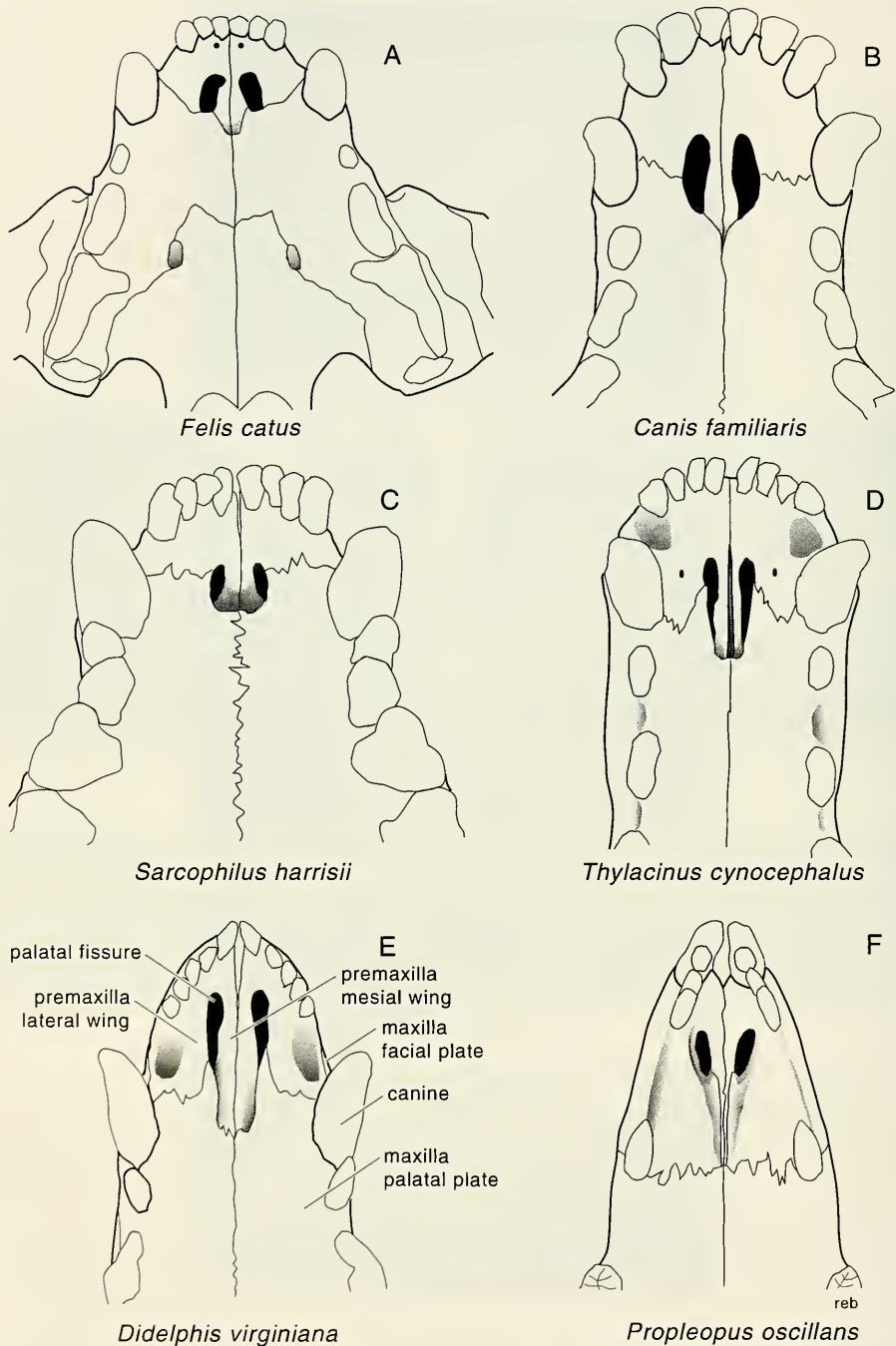
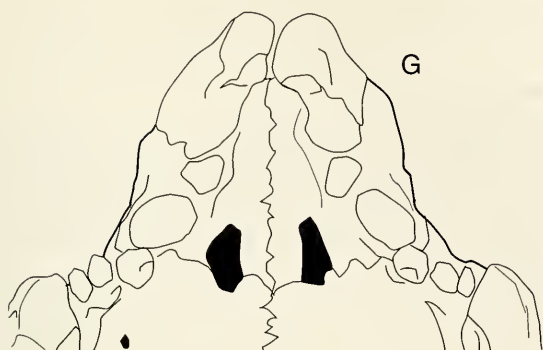
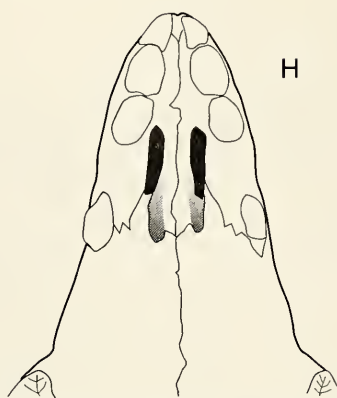
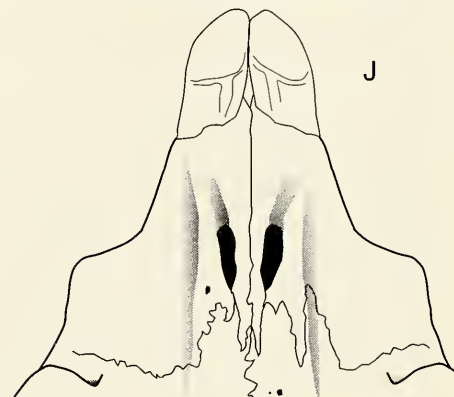
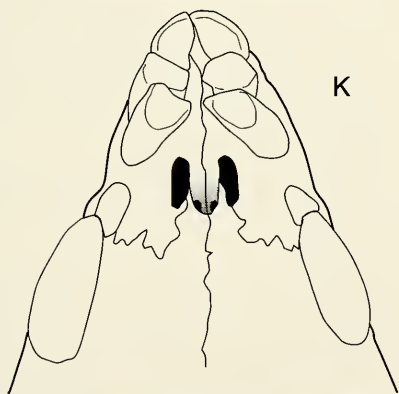
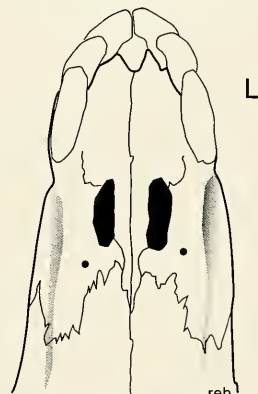


Figure 19. The premaxillary palate of *P. oscillans* (F) compared with short-faced and long-faced Carnivora (A, *Felis catus*; B, *Canis familiaris*); short-faced and long-faced polyprotodont marsupial carnivores (C, *Sarcophilus harrisii*; D, *Thylacinus cynocephalus*); a short-faced diprotodont carnivore (G, *Thylacoleo carnifex*), and short-faced and comparatively long-faced diprotodonts of different lineages

*Thylacoleo carnifex**Hypsiprymnodon moschatus**Phascolarctos cinereus**Vombatus ursinus**Aepyprymnus rufescens**Macropus giganteus*

(I, *Phascolarctos cinereus* and J, *Vombatus ursinus*; K, *Aepyprymnus rufescens* and L, *Macropus giganteus*). H, *Hypsiprymnodon moschatus*, illustrates the possible plesiomorphic condition in Hypsiprymnodontidae. *Didelphis virginiana*, E, (with very similar sutural relations to *Hypsiprymnodon*) illustrates the probable ancestral condition of all marsupials.

## DISCUSSION

**Functional inferences from cranio-dental morphology**Premaxilla, incisors and the diastema (Figs 2, 19):

The premaxilla, although elongate, is strongly united with the maxilla by a deeply serrate scarf joint. The break in left maxillary fragment of P35632 just anterior to the suture, instead of separating along the sutural line, demonstrates its robustness. Regrettably, insufficient of the facial surface of the premaxilla is preserved to provide useful information on its facial junction with the maxilla.

Palatal fissures are positioned about mid-way along the premaxilla and separated from the maxillo-premaxillary suture (Fig. 19F). Each fissure lies within a groove bounded by ridges. The interpremaxillary suture is finely serrate. The lateral and mesial wings of the premaxilla are closely sutured posterior to the fissure. Posterior to the fissure the mesial wing is a very slender bone interposed between the lateral wing and the interpremaxillary suture.

The ancestral condition in marsupials (exemplified by *Didelphis* and *Hypsiprymnodon* in Fig. 19E, H) seems, on the basis of its wide distribution<sup>6</sup> among members of the major marsupial taxa, to be one in which fissures are elongate and the lateral and mesial wings do not meet behind them. Moreover, the mesial wings do not suture laterally with the maxilla. Thus, the median part of the premaxillary palate, along the maxillo-premaxillary suture, from one fissure to the other (about 1/3 of the width of the palate in *Didelphis* and *Dasyurus*) is a major zone of weakness in the junction between the four elements; presumably its strength depends to a great extent upon the scarf joint between the elements facially. The premaxillae of marsupial fossils are frequently detached from the skull at this point.

In both short and long-faced Carnivora (exemplified by cats and dogs, Fig. 19 A, B) the incisors, which are placed wholly in the premaxilla, are used for pulling and some cutting, while the canines placed immediately behind the maxillo-premaxillary suture are used for pulling, slicing (i.e. shearing) (Van Valkenburgh 1996) and holding. In both groups of carnivores, the incisors are placed transversely and the palatal plate of the premaxilla is shortened bringing the incisors close to the canines. Both the lateral and mesial wings of the premaxilla are firmly sutured with the maxilla. Polyprotodont marsupials appear to adopt the same solution as Carnivora when incisors and canines are required for similar use. Thus, a similar arrangement of the incisors and a shortening of the premaxillary palate (but without as close a suture between the mesial wings of the premaxilla and the maxilla) occurs in *Sarcophilus* and *Thylacinus* (Figs 19 C, D).

In diprotodont marsupials, because of the form of the mandible, canines have no interlocking partners with the result that the canine function of polyprotodonts, if required, must also be performed by the anterior incisors with concomitant strengthening of the palate between the premaxilla and the maxilla.

Different clades have accomplished this in different ways. Thus, in the carnivorous marsupial lion *Thylacoleo* (Fig. 19G), which is structurally analogous with the cats, the maxilla is shortened and broadened but, comparatively, the premaxilla is less reduced than in cats and accommodates the enlarged  $I^1$  which becomes greatly elongate dorsally within a tall premaxilla which is sutured facially with the maxilla closely behind the  $I^1$ ; both this suture and the naso-premaxillary suture are closely serrate. The palatal maxillo-premaxillary suture is broad and serrate also. The posterior ends of the mesial wings of the premaxilla are united in the palatal suture.

The wombats retain a wide diastema (and in that sense are long-faced) but possess greatly enlarged  $I^1$ s that insert deeply within the premaxillae. There are also strong longitudinal ridges lateral to the recessed palatal fissures. On the basis that palatal ridges



and recessed fissures are possessed by both long-faced (e.g. *Vombatus*, Fig. 19J) and short-faced vombatiforms (e.g. *Phascolarctos*, Fig. 19I) it is probable that these ridges are synapomorphic in vombatiforms. In the wombats the palatal fissures are deeply recessed, the most extreme development occurring in *Phascolonus* (see Ride 1967, fig. 2B). The mesial wings of the premaxilla are also united with the maxillae at a short but strong suture. In *Phascolarctos*, with relatively small  $I^1$ s, the posterior ends of the mesial wings are less strongly united, the palatal fissures are less recessed, and the  $I^1$ s do not extend postero-laterally to the maxilla. The three pairs of incisor, together, function as a grasping unit extending posteriorly along most of the premaxilla.

In *Aepyprymnus* (Fig. 19K), a short-faced rhizophagous potoroid macropodoid, the  $I^1$  is elongate posteriorly and lies mesial to the canine as in *P. oscillans* (Fig. 4A, D). The palate is without ridges but parallels the structure in *Thylacoleo* in being broad. The mesial wings of the premaxilla are united with the maxilla at the maxillo-premaxillary suture. In the long-faced macropodiforms (e.g. *Macropus* Fig. 19L) the  $I^1$ s are short, do not extend posteriorly, but, presumably to meet the requirements of grasping with the  $I^2$  and  $I^3$ , in large long-faced species (e.g. *M. giganteus*, *M. fuliginosus* and *M. antilopinus*) the premaxilla is strengthened in an analogous manner. The palatal fissures are anterior to the maxillo-premaxillary suture and the mesial and lateral wings of the premaxillae fuse behind them.

Like the incisors of *Vombatus* and *Aepyprymnus*, the  $I^1$ s of *P. oscillans* are elongate within the premaxillae (extending posteriorly to the maxillae). Strengthening of the premaxilla (Fig. 19F) is also achieved by the development of vombatiform-like lateral ridges and recessed palatal fissures, but even more than in other diprotodonts, the palatal fissures are distanced from the premaxillo-maxillary suture and strengthened behind as well by the firm union of the lateral and mesial wings. The maxillo-premaxillary suture is not interrupted by the mesial wings as it is in *Macropus*. If *Hypsiprymnodon* is taken to represent the ancestral condition of the Hypsiprymnodontidae, all these features listed in *P. oscillans* (elongated first incisors, recessed palatal fissures, lateral ridges, anterior placement of the palatal fissures, strongly united lateral and mesial wings) constitute adaptational responses to a specialized masticatory function in an animal which did not become short-faced but to which considerable incisor force was necessary.

$I^1$  and  $I_1$  have sharp chisel edges maintained by a combination of differential hardness of dental tissues and wear. The teeth are open rooted (probably persistently erupting). Enamel and dentine is distributed in a manner that, on wearing (and possibly also by thegnosis) maintains the edges<sup>7</sup>. Macroscopically, they appear only slightly damaged, implying either that food substances are soft and relatively grit-free, or that the sharp edges are maintained as the result of rapid replacement of tooth substance from the open roots together with active incisor thegnosis.  $I^1$  are more proodont than in rhizophagous forms such as *Aepyprymnus* and *Vombatus*. In *Vombatus* the single pair are flattened; in *Aepyprymnus* the flat surface area of the upper incisors as a group is increased by flattening of the broad  $I^1$  and  $I^2$ . In both genera they serve as excavating and pulling tools. In feeders on hypogeal fungi such as *Bettongia* and *Potorous*, incisor edges are more obtuse and possibly less liable to damage by grit while excavating.

$I^{2,3}$  of *Propleopus oscillans* are small and placed closely behind  $I^1$ , roots are angled posteriorly, and (from the small size of their alveoli) were much less tall, probably resulting in a sharp beak-like incisor complex which occluded with the sharp, anteriorly directed, edges of the upward-facing  $I_1$  in the mandible which, from the genial pit, is angled upwards. This angle carries the incisor tips almost to the level of the molar row. Unlike the larger grazing and browsing Macropodidae, the premaxilla is not flexed downwards to meet horizontally placed lower incisors as in kangaroos and wallabies (Ride 1959) in which maximum surface for grasping is achieved by opposing the antero-posteriorly elongate edges of the group of upper incisors to the lateral edges of the procumbent lower incisors.

The anterior incisors are also quite unlike those of placental chisel-tooth diggers (Hildebrand 1985b) and it seems clear that *P. oscillans* was not specialized for excavating food from soil with these teeth. On the other hand, incisors could certainly have combined the piercing, shearing and holding functions of the incisors and canines of the Carnivora (Van Valkenburgh 1996).

The upper canines are rooted in the maxillae. They are not elongate (Table 1) and would have been only approximately as tall as  $I^1$  and  $P^3$ . Nevertheless, they are antero-posteriorly ridged and robust and were placed mid-way in the short diastema. They have no opposing lower equivalents and their function must have been in holding rather than shearing as in Carnivora.

The infraorbital canal is large and placed midway along the face above the anterior edge of the premolar. It transmits branches of cranial nerves V2 (sensory from skin and rostrum) and VII. Both the large size of the infraorbital foramen and the anterior palatal fissures imply that the muzzle had important sensory functions.

The cheek teeth, commencing with the sectorials, follow shortly after the canine, implying that capacity to manipulate numerous ingested particles (as in Macropodinae, Ride 1959) was of less importance than the ability to grasp and hold larger items. However, despite the shortened diastema, the face is long both to the orbit and to the anterior edge of the adductor attachments of the mandible (the masseteric process), probably enabling wide gape characteristic of high amplitude jaw movement and enabling-puncture crushing (crack-propagation in hard brittle food materials) to take place well back in the unreduced molar row. Sectorial function is carried well forward in the open mouth and well anterior of the orbit.

High amplitude jaw movement has been shown in experimental studies to be characteristic of opportunistic feeders (omnivores) and carnivores such as the opossum (*Didelphis*), tenrec and cat, and not of herbivores (see Hiiemae and Crompton 1985, p. 282). From photographs, *Thylacinus* has an exceptionally wide gape and on the basis of its unreduced molar row and dental topography had a similar high amplitude of movement.

#### Occlusal relationships of cheek-teeth:

##### Premolars:

Large ridged sectorial premolars, which originally suggested carnivorous habits for *P. oscillans*, occur widely among the modern Australian marsupial fauna. Among modern macropodiforms they occur in *Hypsiprymnodon* and all genera of Potoroidae; among Burramyidae they are characteristic of *Burramys*. Recent studies of the diet of these animals indicate that it is unwarranted to infer a carnivorous habit from the possession of ridged sectorials alone. Moreover, closer examination reveals that to emphasize size, ridging and lateral compression, as is done when speaking of such teeth as a class of "plagiaulacoid premolars", conceals fundamental morphological differences between the teeth in different groups and in their functioning (Ride and Heady in prep.) Studies by Bennett and Baxter (1989), Scotts and Seebeck (1989), Claridge et al. (1993), Christiansen (1980), Taylor (1992), and Seebeck et al. (1989) indicate that potoroids are, mostly, primarily mycophagous, the exception being *Aepyprymnus* which is primarily rhizophagous. All take some arthropods and some (*Bettongia lesueur* and *B. penicillata*) are known to take flesh. The much smaller *Burramys parvus* (c. 40 g) is an insectivorous omnivore (Mansergh et al. 1990). Its major food is the Bogong moth, *Agrotis infusa*. Vegetative material amounts to about 16% of the diet. Bogong moths are seasonal and seeds with hard seed coats are cached and eaten in winter. The sectorials have been observed in use in cracking the seed coats.

From the evidence of microwear, it is clear that the sectorials of *P. oscillans* were used both in shearing and crushing and that these functions were primarily carried out in different parts of the tooth.



No paired adult tooth rows are available for articulation, but the molars of specimens P20815 and Qd Mus F6675 occlude virtually perfectly. In these, the height of the crest of P<sub>3</sub> above the molar cusps enables a tooth-on-tooth contact between opposing premolar ridges from ridge E, posteriorly, to be obtained by rotating the ventral border of the ramus mesially accompanied by slight condylar displacement. The shape and distribution of the articular surface on the transversely cylindrical condyle indicates that it could have moved forward in an anteriorly unrestricted glenoid, but suggests that movement of the mandible would have been restricted posteriorly by a closed bearing concavity on the anterior surface of the post-glenoid process. The extensive rugose mandibular symphysis indicates that relative rotational movement between the rami was possible. Tooth-on-tooth contact can be made also at the lingual boss. The worn wear facet of the P<sub>3</sub> of the holotype (Qd Mus. F3302) corresponds with the area of premolar tooth-on-tooth contact estimated from occluding the premolars of the other two specimens.

In the younger animal P35632, in which both upper and lower tooth rows are present, when the molars are occluded, the upper and lower sectorial premolars are separated by a distance equal to about half their widths. At this stage of growth, the crests of the sectorial premolars (P<sub>2</sub>) are at the same level as the cusps of the deciduous premolars and only a small area of the sectorial is brought into tooth-on-tooth contact by rotating the rami.

Evidence of puncture crushing of brittle items whereby cracks are propagated occurs along the premolar crest, at the molar-premolar junction (Fig. 17) and particularly on the rounded cusps of the molars (see interpretation of Figs 21 and 22). However the principal function of the cuspidate crests of the premolar was probably that of high amplitude shearing<sup>8</sup> of tough fibrous material such as hide, tendon or aponeurosis, while abrasional damage incidentally resulting from puncture crushing at the cusps is probably the result of the inclusion of hard resistant material (such as grit or bone) within the material shorn. In this way the crests would have been used in a manner functionally analogous to the shearing carnassials of fissipede carnivores. However, the relatively small number of short features (pits and gouges) and the relatively high degree of long feature orientation (Ride and Heady in prep.), indicate a diet such as that of flesh eaters or moderate bone eaters in which puncture-crushing occurs only at, and deliberately in, a different part of the tooth row as illustrated for the wolf by Van Valkenburgh, Teaford and Walker (1990).

At first sight, the premolar ridges suggest that the tooth had a file-like multi-bladed shearing capability. However, in both upper and lower premolars the acute edges of ridges face posteriorly (Figs 14, 15) and are not opposable. At the wear facets of ridges where tooth-on-tooth contact is obtained, the principal effect seems to have been grinding (analogous to milling) in which flat surfaces adpress material between them without sharp edges shearing past each other. Although tooth-on-tooth contact is not obtained within the channels between the ridges, tough fibrous material shorn at the crest and pressed into, and being forced along, a channel of P<sub>3</sub> to the lingual boss would probably have been intersected obliquely by the sharp edge of a ridge of P<sub>3</sub> even though the edges of ridges may not cross each other. Within the channels (Figs 15, 16), directional wear demonstrated by abrasion grooves is mostly along the channels. Anteriorly on the premolars, where there was no tooth-on-tooth contact, abrasion features of the sort that can be interpreted as wear of enamel by soft material indicates that soft-tissues may have been parted by penetration by this part of the tooth in extension of the aperture made in the food by the posterior part of the blade.

The uniform width of abrasion grooves and a general trend along the wear facets of the ridges (Fig. 12) imply uniform pressure on inclusions and orthal occlusion, whereas the irregularity of grooves in the channels imply that the inclusions were less rigidly held. It is possible that a function of the channels was to accommodate such irregularities.



The development of wear facets along the apical part of the hindmost ridges of the premolars of *P. oscillans*, followed by extension of wear both forward and away from the crest, is similar to the pattern of wear described by Stirat (1981) in *Burramys parvus*, a small phalangeroid with very similar premolars. As in *P. oscillans*, the relative movement of the occluding premolars is orthal in the direction of the ridges. At the posterior end of the premolar, topographic differences produce differently-shaped facets. In wild-caught specimens of *B. parvus* there is very little wear of the cusps – even in the case of individuals with extensive wear facets (captive specimens develop considerable cuspal wear). The sequence of facet development in *Hypsiprymnodon moschatus* is also similar (Ride and Heady in prep.). In  $P_3$  it is virtually identical, but in  $P^3$  the facet commences as a depression “scooped out” of the surfaces of the posterior ridges about a third of the distance below the crest (the development of wear facets in  $P^3$  of *P. oscillans* is not yet known). In *H. moschatus* posterior cusps and ridges are abraded extensively as in *P. oscillans*. The general trend of movement is also orthal (Ride and Heady in prep.).

By contrast, development of premolar wear facets in Potoroidae is different, although in all species studied the direction of occlusal movement is also orthal. Morton (1981) has studied *Potorous tridactylus*, *Aepyprymnus rufescens* and *Bettongia gaimardi*. In *P. tridactylus*, which has elongated premolars oriented in line with the molar row, and dominant anterior and posterior premolar cusps (higher than those between) and rounded ridges, wear is initially confined to the tips of the anterior and posterior cusps of the occluding surfaces and then spreads to the cusps between. Facets develop on the ridges. Cavitation commences immediately below the cusps and exposed dentine surfaces spread along the planar facets developed on the ridges. The area of exposed dentine becomes continuous and a bevelled edge develops along the length of the tooth. The process continues until both cusps and ridges are obliterated. In *A. rufescens*, the premolars are “toed inwards”, their anterior ends being directed mesially. Ridges are numerous and more acute than in *P. tridactylus*. A wear facet develops, but instead of spreading along the ridges as in *P. tridactylus* and then becoming continuous along the tooth, the facet develops as a bevelled surface on which dentine is exposed. As it wears the tooth retains its cuspal margin resulting from the tips of the ridges of the non-occluding face being exposed progressively along the edge. In *Bettongia gaimardi* the development of the facet is as in *A. rufescens*, but becomes wedge shaped, narrowing anteriorly. The premolars are “toed outwards” i.e. set at an angle to the molar rows, with their anterior ends angled buccally. Morton considered that the shape of the facet is due to the posterior part of the tooth coming into occlusion first.

In all Potoroidae studied, premolar facet development is accompanied by dentine exposure and the development of a bevelled edge which Morton argues is to enable a “relief angle” to be maintained between opposing edges of the blades. She also regards the presence of crenulations and cusps in such teeth as enabling bite force to be more effectively applied at a reduced occlusal area.

Confirmation that premolar function in Potoroidae is orthal and combines both puncture crushing and shearing is supplied by cinefluoroscopic studies of mastication in *B. penicillata* (Parker 1977). In crushing, Parker observed that blades are approximated directly in line with each other. Approximation coincides with anteriorwards condylar movement at the contralateral condyle accompanied by some relative movement at the symphysis. During crushing there may be slight anteriorwards movement of the ipsilateral condyle. The puncture crushing movement may be repeated several times in succession. In shearing, the mandibular blade passes on the median side of the maxillary blade. Observations did not distinguish whether puncture crushing was confined to a particular part of the tooth, which we postulate in *P. oscillans*, but Parker did observe careful manual positioning, and repositioning, of objects for puncture crushing which implies that a particular part of the premolar is favoured.

*B. penicillata*, like *P. oscillans*, has “toed out” premolars and the general form of

wear facet development is similar. It seems probable, despite differences in morphological detail, that the dual functions of shearing and crushing were performed in a similar manner and in similar parts of the tooth. SEM studies of *B. penicillata* directly comparable with those reported here for *P. oscillans* are in progress (Ride and Heady, in prep).

### Molars:

The molar row is scarcely reduced posteriorly. There is no indication of a transverse or antero-transverse component in chewing as in frugivores and folivores (*Aeteles*, Kay and Hiiemae 1974; *Colobus*, Teaford 1986; *Oryctolagus*, Ardran et al. 1958; *Macropus*, Ride 1959; *Macropus*, Wallabia, Sanson 1980), granivores (*Rattus*, Hiiemae and Ardran 1968) or mycophagous animals (Potoroinae, Parker 1977; Morton 1981); rather the power stroke of the gape cycle seems to have been more or less vertical in direction in both premolars and molars (Figs 12, 13, 21) - closer to that found in carnivores but not herbivores (Hiiemae and Crompton 1985, p. 280) (Fig. 23).

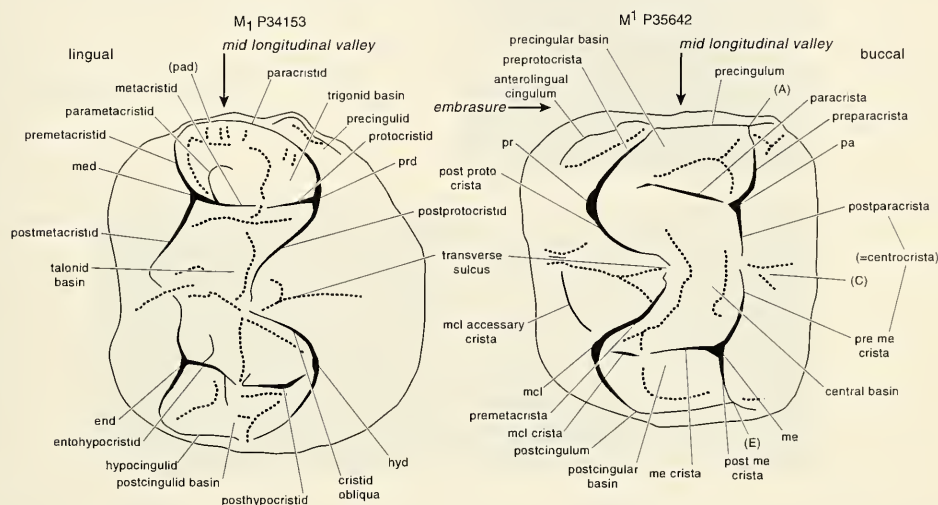


Figure 20. *P. oscillans*, molar cusps and crests. Key to conventions for cusps, crests, and grooves, and to topographical nomenclature employed.

Abbreviations: end = entoconid, hyd = hypoconid, pa = paracone, pad = paraconic, pr = protocone, mcl = metaconule, me = metacone, med = metaconoid, prd = protoconoid.

When the molars of the paired mandibles and maxillae (P35632, P35633; and also P20815, F6675) are occluded so that the protocones of the upper teeth lie in the trigonid basins of the lower molars (Fig. 22), the cusps and basins interlock. The buccal cusps of each lower tooth (protoconid and hypoconid) insert into the basins of the mid-longitudinal valley of the opposing tooth row (i.e., the buccal cusps of  $M_2$  insert into the postcingular basin of  $M_1$  and the central basin of  $M_2$  respectively). The lingual cusps occlude within accessory structures (the metaconule accessory crista and anterolingual cingulum) along the lingual margin of the upper molars (i.e., the metaconid of  $M_2$  bites into the mesial embrasure between the metaconule of  $M_1$  and the anterolingual cingulum of  $M_2$ , while the entoconid bites into the sulcus of  $M_2$  antero-mesial to the metaconule, fitting between its postprotocrista and metaconule accessory crista).

This rather precise fit and interlocking of cusps in *P. oscillans* seems to indicate only limited transverse or antero-transverse molar movement occurred as is observed in



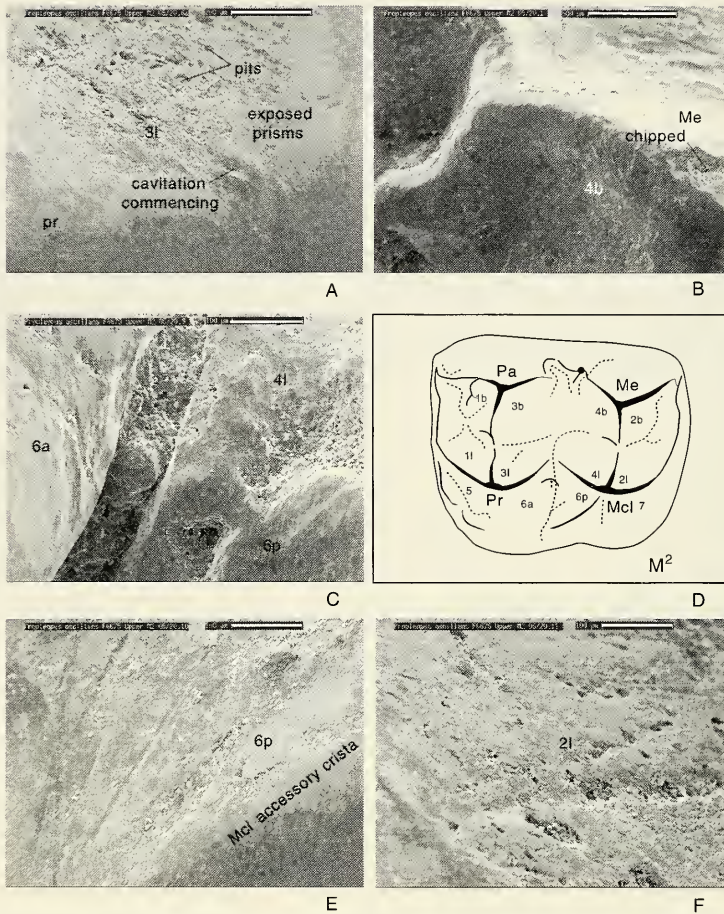


Figure 21. Shearing and crushing features in the *P. oscillans* molar ( $M^2$  of F6675). D: diagram based on outline of unworn P18541 to indicate the positions of areas of wear relative to cusps and crests. The numerical designation of the areas adopted here is an extension of the facet designations of Hiiemae and Crompton (1970, fig. 4) for *Didelphis marsupialis* (probably *D. virginiana*) and Kay and Hiiemae (1974) for fossil and modern primates. Numbering on the primary cusps (Pa, Me) and on the lingual face of the protocone (Pr) is the same. Other areas are numbered differently from the facet notation of these authors, to avoid any inference that the hypocone of primates and the metaconule of quadricuspid diprotodont marsupials are homologues. Accordingly areas on the buccal surface of the protocone (Pr) and metaconule (Mcl) are numbered as though the facets on the primary cusps of *Didelphis* had been divided. Thus, the letters b (buccal), l (lingual), a (anterior), p (posterior) are added to facet number to designate the components. Facet 9 of primates may be equivalent to all of areas 11-41. Other abbreviations: Pa (paracone), Me (metacone). White scale bar in A = 200  $\mu$ m, B = 500  $\mu$ m, C = 100  $\mu$ m, E = 100  $\mu$ m, and F = 100  $\mu$ m.

Interpretation.- A: buccal surface of protocone (lower left corner) and area 3l; the protocone is a rounded crushing cusp. Cavitation is commencing on the postprotocrista close to the apex, abrasion pits are evident. Abrasion grooving extending onto the lingual surface on area 6a (a shearing surface) is visible along the postprotocrista (compare with Teaford 1988b, fig. 8). B: lingual face of premetacrista and area 4b; fracture of the tip of the pointed metacone indicates the vulnerability of pointed cusps to damage; abrasion grooves extend vertically from the ridge of the premetacrista onto the face of area 4b (a shearing surface); pits towards the base of the surface show where the rounded hypoconid occludes (a crushing surface). C: wear surfaces on either side of the sulcus between protocone and metaconulid. Pits and exposed prisms occur on the anterobuccal surface of 4l (a crushing surface), grooves extend vertically from the edge of the premetaconulecrista (bottom right) onto surface 6p (a shearing surface), and on surface 6a anterior to the sulcus. E: Parallel abrasion grooves and gouges in area 6p (a shearing surface) on the buccal face of the metaconule accessory crista. F: buccal surface of metaconule and area 2l (a crushing surface); as in the protocone, the metaconule is a rounded crushing cusp; cavitation is commencing at the tip (bottom left), abrasion pits and gouges from crushing on surface 2l are evident.



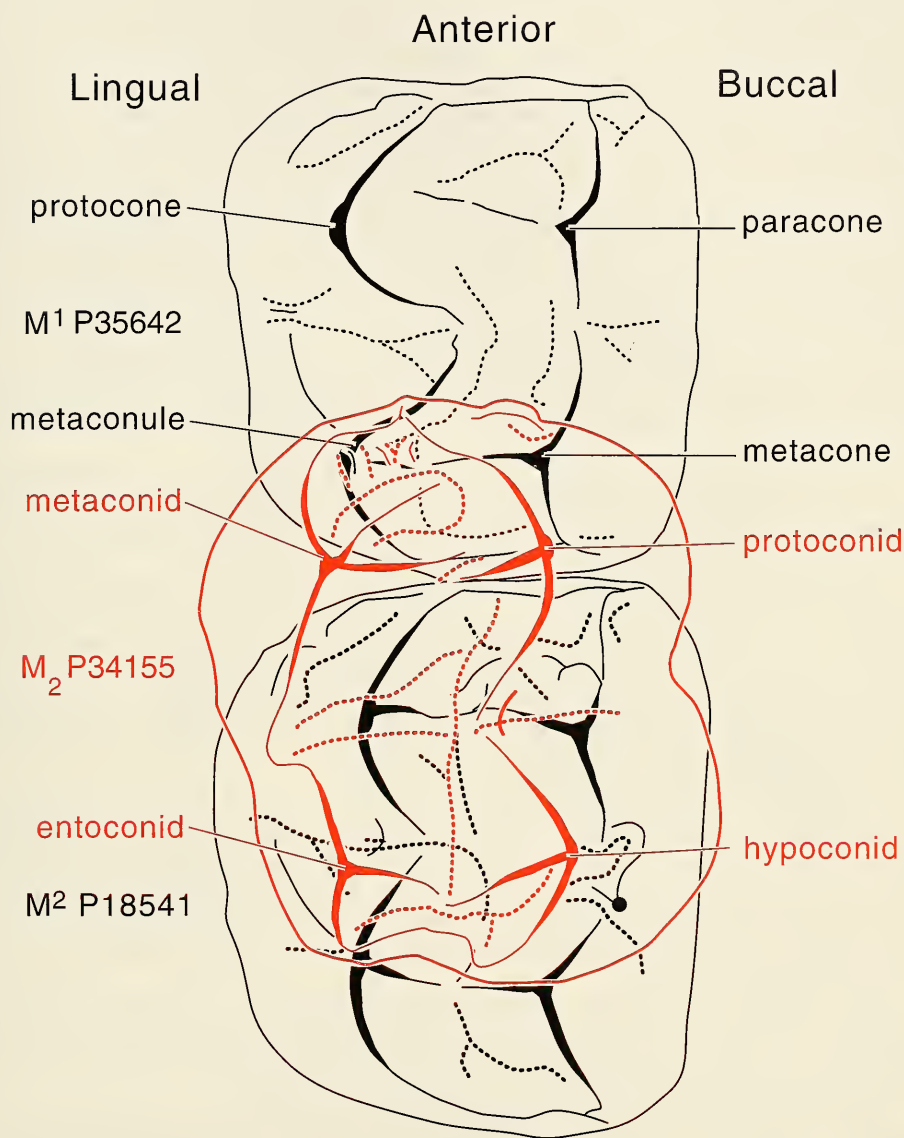


Figure 22. Occlusal relationships between the upper and lower molars of *P. oscillans*. The molars are aligned approximately representing the commencement of the power stroke (Phase I) (see Fig. 21 for SEM illustrations of the different forms of shearing and crushing cusps and wear surfaces). Rounded crushing cusps are aligned so that they occlude within the mid-longitudinal valleys of opposing teeth. Shearing crests of both upper and lower molars are aligned along the external (lingual and buccal) margins of the tooth-rows. Thus, in the upper molar, shearing surfaces on the acute anteroposterior ridges of the paracone and metacone shear against surfaces on the buccal faces of the rounded protoconid and hypoconid. The latter rounded cusps occlude within the rugose basins of the median longitudinal valley. The similarly rounded protocone and metaconule occlude in the same manner.

folivores, frugivores and omnivores. In animals with such diets the power stroke contains two phases defined by Kay and Hiimae (1974). Phase I begins as the buccal surfaces of the lower molars are brought into contact with the buccal surfaces of the upper molars, and continues until the protocone is located in the talonid basin (the position of centric occlusion). From centric occlusion the movement continues until the antero-mesial movement of the lower molars carries them out of occlusion. This second, post-centric phase is defined as Phase II. Both cinefluoroscopic and microwear studies of a wide range of folivores, frugivores and omnivores (referred to above) have revealed that Phase II of the power stroke is extended into an anterolingual grinding movement (Kay and Hiimae 1974). Thus the upper lingual cusps of leaf-eating and fruit-eating monkeys become flattened and wear facet 9 buccal to the protocone becomes greatly extended in area (see *Ateles*, fig. 4D of Kay and Hiimae, loc. cit., also see Teaford 1986; for analogue of wear facet 9 in *P. oscillans* see text Fig. 21). In other folivores, especially grazers and browsers, serial arrangement of cutting crests (as in lophodont and selenodont animals) provide shearing and grinding mechanisms.

In carnivores, Phase II of the power stroke is greatly reduced (Hiimae and Crompton 1985, p. 280). Anterior movement is virtually eliminated and movement during the power stroke is confined to Phase I and is more or less vertical in direction (Fig. 23).

In *P. oscillans*, due to its rarity, it has only been possible to study the molar microwear in a single maxilla (F6675) but conclusions from this agree so closely with the conclusions derived from the gross morphology that there is little doubt that they will be found to be generally applicable (see text accompanying Fig. 21).

The function of the buccal cusps and cristae are exemplified by the metacone and premetacrista illustrated in Fig. 21B; its anteromesial face has exposed enamel prisms while the crest along its margin is grooved with vertical abrasion; the metacone is chipped. The lingual cusps and their surfaces (protocone and metaconule, Fig. 21A, F) reveal pits and gouges typical of puncture crushing surfaces. The trend of the gouges is back into the median longitudinal valley. Despite the fact that the specimen is fully adult the rounded buccal cusps are not diminished in height as compared with the pointed buccal cusps although cavitation is commencing at their tips.

The function of the lingual accessory structures is exemplified by anterolingual abrasion grooving in the channel between the premetaconulecrista and the metaconule accessory crista (Fig. 21E). The abrasion grooves run along the channel – not across the metaconule accessory crista. The sulcus between the protocone and the metaconule (Fig. 21C) is not traversed by abrasion grooves or gouges as they would be if it was subject to the passage of a lower cusp moving anteromesially through it. Instead, it presents a typical crushing abrasion surface.

In conclusion, the features of the microwear support the contention that relative movement of the molars was orthal with a slight anteromesial component as would be expected in an occlusal cycle with the power stroke virtually confined to Phase I and in which both lingual and buccal cusps were simultaneously engaged.

In the occluded tooth rows, the lingual-most and buccal-most rows of cusps would have been primarily shearing in function (although, inevitably, some crushing must have taken place in them as revealed by the chipping of the metacone in Fig. 21B). The two rows of rounded cusps occluding between them were specialised crushing eminences; they also provided rounded shearing surfaces against which the crests of the “shearing” cusps worked.

The combination of both shearing and crushing capability along the tooth row is analogous to that found in Thylacinidae, but not directly comparable because *P. oscillans* also possessed a “carnassial equivalent”. It is also possible that the facet on the posterolingual face of the premolar and its junction with M1 may have provided it with a dental position at which particularly large objects might have been puncture crushed



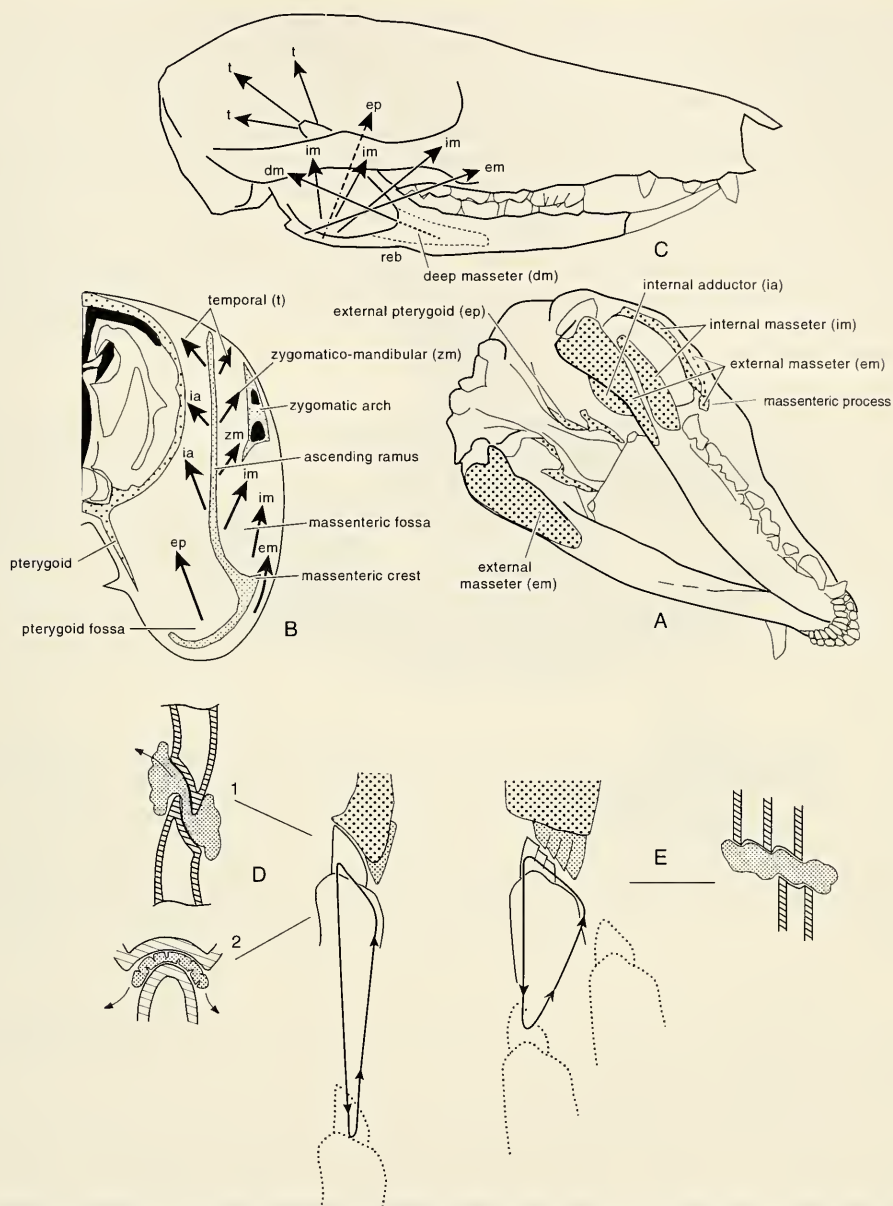


Figure 23. Adductor muscles of mastication in marsupials; the gape cycle; and the elements of tooth design (for shearing and crushing). A: *Didelphis virginiana*, origin and insertion of the components of the masseter-ptyergo-temporal mass; stipple indicates areas of attachment (modified from Hiiemae and Jenkins 1969). B: *Macropus agilis*, directions of action of muscle components in the transverse plane at the level of the ascending ramus (after Ride 1959). C: *Potorous tridactylus*, directions of action of muscle components in the longitudinal plane; the insertion of the deep masseter within the masseteric canal, and the external pterygoid mesial to the ramus, are shown in broken line (constructed from Morton 1981). D: high amplitude gape cycle typical of carnivores with small lateral component in the power stroke; 1.- shearing of soft, tough, materials between crests and facets (e.g., hide, muscle, or leaves); 2.- crushing hard, brittle or turgid materials between blunt cusp and basin (puncture-crushing involves propagating a crack from an initial crush fracture, e.g., as in bone). E: low amplitude gape cycle with large mesial component in the power stroke typical of mammals that feed on tough fibrous material (e.g. vascular bundles in leaves and grasses) by shearing it between series of sharp edges (D and E modified from Hiiemae and Crompton 1985).

preferentially. It is also probably relevant that studies of free-ranging long-faced Carnivora (dogs) revealed that the carnassials (here the analogue of the part of the sectorial premolars anterior to ridge A) are used to cut skin and muscle while bones are cracked by the blunt cusps of the postcarnassial molars (Van Valkenburgh 1996).

On the basis that *P. oscillans* possessed an elongate molar row and proportionately smaller premolars than other *Propleopus* [and *Ekaltadeta*], Wroe (1996) considered that *P. oscillans* was more herbivorous and less carnivorous than the others. This view is not supported. Wroe (and all those engaged in the controversy over the diet of *Thylacoleo*) based arguments on short-faced Carnivora (e.g. *Felis*), but carnivores can equally be long-faced (e.g. *Vulpes*, *Canis*, etc.), and as demonstrated by *Thylacinus*, shearing and puncture-crushing may be distributed along the entire unreduced molar row. In view of the high placement of the mandibular condyle in *Ekaltadeta ima* (see below) that species may have been less carnivorous than *P. oscillans*.

#### Masticatory musculature and gape cycle:

The deep but short and narrow zygomatic arches, the low, rounded, masseteric processes of the maxillo-jugals, and the rather shallow masseteric fossae and crests of the dentaries, when taken together with the wide coronoid processes, that is *Thylacinus*-like in shape, and the well developed pterygoid fossae, imply that the external masseter<sup>9</sup>, and the superficial layers of the internal masseter (see Fig. 23) muscles played a relatively small part in mandibular adduction as compared with the temporal and external pterygoids. In macropodine and potorine mastication in which the mesial component of the power stroke is large (Phase II), the external masseters play an important part (Ride 1959; Morton 1981; Parker 1977); their direction of action is such that they must have a major role in centralizing the mandible through the power stroke into minimum gape (Fig. 23C).

On the other hand, the great size of the masseteric canal within the body of the dentary, and its forward extension to the level of the posterior end of the premolar, implies that the deep masseter within it strongly reinforced the rearward closing action of the temporal on the mandible and the maintenance of pressure on the occlusal faces of the premolars during the power stroke. Together with the temporal, external pterygoid, relatively small external masseter, and median layer of the internal masseter and the internal adductor and zygomatico-mandibular (Fig. 23B), it would also have played an important part in controlling the vertical orientation of the lower premolar (see Sanson 1989).

Although the glenoid fossa is not known, these inferred muscular proportions, together with the cylindrical posterior face of the condyle, imply strong rearwardly directed muscular forces acting on the condyle during the power stroke requiring a robust post-glenoid process. The direction of abrasion features at the cusps of the premolars (Figs 10, 11) support this interpretation.

The low position of the condyle relative to the mandibular tooth row (at the level of the crest of the sectorial premolar) implies both wide gape and a capacity to apply point shearing as occurs in Carnivora where particularly resistant objects are shorn or puncture-crushed at particular positions along the tooth row defined by the different morphologies of different teeth (see Van Valkenburgh 1996). *Thylacinus* and *Sarcophilus* with little morphological difference between anterior and posterior molars have the same capacity. This may indicate that, even though shearing and puncture-crushing may have taken place anywhere along the molar row, there may have been preferred positions according to the gape and force required to crush any particular object.

It is characteristic of mammals with transverse (or semi-transverse) shearing distributed over large areas of tooth surface, that there is a large mesial component in the power stroke of the gape cycle (Phase II). This occurs especially in herbivores (Fig. 23E). In cases where much of the molar row can be occluded more-or-less simultaneous-



ly, the condyle is located above the molar row (see Sanson 1989 figs 4-7). In herbivores the widths of upper and lower molars are usually widely discrepant also (but not always e.g. *Phascolarctos*). Among Hypsiprymnodontidae the position of the condyle appears primitively to have been moderately high. *H. moschatus*, *H. bartholomaii* (see Flannery and Archer 1987, fig. 2), *Ekaltadeta* (Archer et al. 1991, fig. on p. 121) and *Jackmahoneya*, all exhibit a moderately high position of the condyle relative to the tooth row.

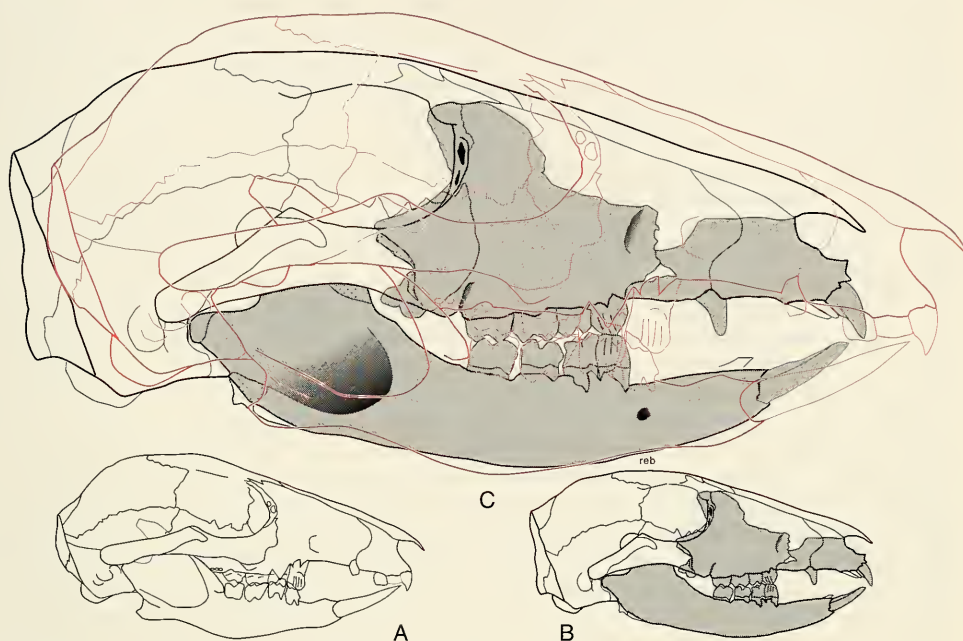


Figure 24. A: lateral view of skull of *Hypsiprymnodon moschatus* at similar stage of dental eruption to the Henschke's Fossil Cave specimen of *P. oscillans*. B: lateral view of reconstructed skull of Henschke's Fossil Cave specimen of *P. oscillans*. C: lateral view of reconstructed skull of *P. oscillans* overlain with outline of skull of *H. moschatus* drawn to the same size (see below for explanation).

#### Overall proportions:

If comparison of skull proportions (Fig. 24) are made with the plesiomorphic condition, changed functions may be inferred from observed differences. *Hypsiprymnodon moschatus* and *Hypsiprymnodon bartholomaii* from the Miocene Dwornamor Local Fauna of Riversleigh (Flannery and Archer 1987) indicate possible plesiomorphic conditions for Hypsiprymnodontidae. *Ekaltadeta* from the same formation, with very much enlarged premolars, reduced molars, and short face, is clearly not plesiomorphic.

Osteological features available for comparison with the material available include the shape of the zygomatic arches, the height of the glenoid above the molar row, and some features anterior to the orbit, and the mandible. Other features of the wall of the braincase, the glenoid and the basicranium are not yet observable in *Propleopus*.

The danger of selecting a phylogenetically distant modern species without fossil intermediates to act as a structural ancestor (or an outgroup from which to determine plesiomorphy and, hence, polarity in apomorphy) is that the characters regarded as plesiomorphic, and hence useful to serve as the start point to a sequence of functional changes, may be apomorphic adaptations and, hence, misleading. However, in this case,

there are good ecological grounds as well as morphological grounds (similarity to *H. bartholomaii*), for considering *H. moschatus* as persistently plesiomorphic. Its meager fossil record supports the assumption that *H. moschatus* continues to occupy its ancestral environment rain forest (whether gallery forest, as suggested by Megirian 1992, or extensive rainforest, as suggested by Archer et al. 1991, is irrelevant).

In its diet and general ecology (see Johnson and Strahan 1982) modern *H. moschatus* also seems almost archetypal of macropodiforms. Considering the alternative possibility that its limb proportions (and hence by implication its general ecology) might be secondarily acquired, Johnson and Strahan (op. cit., p. 42) say, 'when viewed in the context of its other unspecialized characters, it seems much more likely that the Musky Rat-kangaroo is representative of an early stage of evolution of macropods from an arboreal, possum-like stock.'

To examine proportional differences, the skulls of *H. moschatus* and *P. oscillans* were brought to the same size using a ratio between them of 1:3.7. For illustration (Fig. 24) they are aligned on the  $M^2$ . The ratio by which the size of *H. moschatus* was increased for comparison is, firstly, the ratios of the lengths of the entire mandibular rami and, secondly, of the  $M^2$ s. The specimen of *H. moschatus* used for comparison (ANWC CM15551) is at the same stage of dental eruption as *P. oscillans* specimen F35632/3.

The use of the whole mandibular ramus to derive the ratio is open to objection because the structure contains several functional components (length of incisor, length of diastema, size of premolar, length of mandibular cheek-tooth row, breadth of ascending process, length of masseteric fossa), any of which might vary separately to reflect different adaptational needs. Comparison of a single homologous element can be used to test for this disadvantage. Of the characters available  $M^2$  was used because of the molars it is least affected by modifications at the opposite ends of the tooth row (i.e. sectorial specialization and  $M^4$  reduction); it has also been used as a standard for comparison of hypsiprymnodontid dental characters previously (see Ride 1993, fig. 9); Wroe (in press) also independently selected  $M^2$  for a standard of comparison in a study of the evolution of propleopine dental proportions. Comparisons of premolars would have been inappropriate because the premolar has been shown to be evolutionarily labile (Ride, and Wroe, same references). The two methods tried gave closely comparable results (mandibles, 1:3.66;  $M^2$ s, 1:3.7).

From the figure the following proportional differences are apparent. These are expressed as ratios calculated from projections to a line parallel with the palate, or at right angles to that line (values for *P. oscillans* are given first):

- length of premaxilla, not different (44:42);
- length of diastema from centre of canine to anterior edge of premolar, shorter in *P. oscillans* (28:38);
- length from infraorbital foramen to lachrymal foramen, longer (52:28);
- length from infraorbital foramen to masseteric process, longer (58:41);
- length from front of premaxilla to masseteric process, slightly longer (130:121);
- length from front of premolar to masseteric process, longer (58:41);
- zygomatic length, from masseteric process to the posterior edge of the condyle, shorter (84:91);
- zygomatic depth at the masseteric process, much deeper (40:25);

From this comparison, it is seen that *P. oscillans* has a slightly longer face than *H. moschatus* measured from the front of the premaxilla to the masseteric process, but within that, the premaxillary length remains unchanged, the diastema is shorter and the premolars and molars comparatively further forward in the mouth; probably an indication that gape was wider. The anterior part of the jugal at the maxilla is very deep implying, in the absence of strong muscular attachments in the area, a need for distribution of stress from force applied vertically at the cheek teeth (especially on the molar row) greater than



in *H. moschatus*.

The evidence from the masseteric processes that the external masseter muscle had a small antero-posterior action suggests that the structural increase in the depth of the jugal was an adaptation to distribute compressional forces from about the mid point along the molar row. Finch (1982, p. 200) has described bone thickening with a similar implied stress-shedding function from the premolar alveolus on to the anterior border of the orbit and thence to the cranial vault in *Thylacoleo*. If the thickness was maintained along the length of the zygomatic arch it would also have helped to withstand tension stress from the superficial masseter acting vertically on the beam to a much greater extent than in *Hypsiprymnodon*.

The narrow breadth across the zygomatic arches predicted by projecting the surviving anterior portion rearwards (when taken in conjunction with wider zygomatic arch of *H. bartholomaii* than *H. moschatus*, and the much larger ridge on the zygomatic arch for the insertion of the superficial layer of the internal masseter, as compared with *H. moschatus*), suggests also that the external masseters and, probably also the superficial layers of the deep masseter and zygomatico-mandibularis, are secondarily reduced in length in *P. oscillans*. Since these muscles contribute to the production of lateral mandibular movements and the glenoid in *H. bartholomaii* is well dorsal to the molar row, as figured in Flannery and Archer (1987, fig. 2), it is implied that the plesiomorphic condition had an appreciable lateral component and a lesser amplitude shear in the gape cycle.

### Attribution of humeri

Pledge (1981 p.46) described the partial humerus shown in Fig. 7 as straighter, more slender and more cylindrical than those of kangaroos and potorines, and noted that it has markedly reduced deltoid and pectoral ridges and a shorter supinator crest. He pointed out that it bears a much greater resemblance to the humerus of *Hypsiprymnodon moschatus* than to the equivalent element in a range of other marsupials including *Macropus*, *Bettongia*, *Sthenurus*, *Thylacinus*, *Thylacoleo* and *Phascolarctos*.

Our attribution of this bone to *P. oscillans* is based upon similar lines of argument. Firstly, the negative evidence that it is unlike the humeri of any other form presently known from the fossiliferous sediments of Henschke's Fossil Cave. Secondly, the positive evidence that it is morphologically similar to the humeri of *H. moschatus*, the closest living relative of *P. oscillans*.

Aside from *Propleopus* the following marsupial genera are presently known from Henschke's Fossil Cave by cranial material: *Antechinus*, *Dasyurus*, *Phascogale*, *Sarcophilus*, *Sminthopsis*, *Thylacinus*, *Isodon*, *Perameles*, *Cercartetus*, *Petaurus*, *Pseudocheirus*, *Trichosurus*, *Thylacoleo*, *Phascolarctos*, *Lasiiorhinus*, *Vombatus*, *Diprotodon*, *Zygomaturus*, *Palorchestes*, *Aepyprymnus*, *Bettongia*, *Potorous*, *Lagorchestes*, *Macropus*, *Procyonodon*, *Protemnodon*, *Sthenurus* and *Wallabia* (Pledge 1990; John Barrie pers. comm.). Also known from the deposit are the monotreme *Megalibgwilia* (Griffiths et al. 1991) and several genera of murid rodents (Pledge 1990).

Members of most of these genera are far too small to have contributed the humerus shown in Fig. 7. However, nine of the listed marsupial genera include forms in which the humerus approaches or exceeds this bone in size. These genera are now considered.

The humerus of *Thylacinus cynocephalus*, is rather smaller than the bone of Fig. 7, but the Henschke's Cave material contains evidence of a larger form of *Thylacinus*. However, as with *T. cynocephalus*, the humerus of this larger form can be distinguished from the humerus illustrated in Fig. 7 by the very poor development of the supinator crest and greater curvature in the parasagittal plane in *Thylacinus*.

The lack of curvature and/or the very limited development of the pectoral ridge and deltoid crest serve to separate the humerus of Fig. 7 from those of *Thylacoleo*

(Murray 1991, fig. 24), *Diprotodon* (Murray 1991, fig. 21C; Gregory 1951, fig. 18.36), *Zygomaturus* (Scott and Harrison 1911, fig. 1; Murray 1991, fig. 22), *Palorchestes* (Flannery and Archer 1985), *Macropus* (Murray 1991, fig. 26A) and *Sthenurus* (Wells and Tedford 1995). Size and morphology preclude *Procoptodon goliai* (Tedford 1967, fig. 16a; Murray 1991, fig. 26), and as the humeri of the two smaller species of this genus (*P. rapha* and *P. pusio*), which have not so far been described, are likely to be morphologically similar to those of *P. goliai*, we assume that they too are quite unlike the humerus of Fig. 7.

So far as we are aware no illustrations or descriptive accounts have been published of the humerus of *Protemnodon*. However, a Museum of Victoria humerus (NMV P39105) collected from Morwell, and which is almost certainly *P. anak* (Rich pers. comm.), exhibits a number of features which set it far apart from the humeri we attribute to *P. oscillans*. The Morwell specimen, which we have examined, is approximately 255 mm long, but much more massively constructed than the bone of Fig. 7. It has a very strongly developed pectoral ridge which bends mesially over the bicapital groove proximally. The entepicondyle of this bone is well developed and includes a very robust entepicondylar ridge. When this Morwell specimen is viewed from a lateral or medial perspective dual curvature is very evident. Scott and Lord (1924) mention a pair of large humeri (total length 224 mm and 228 mm) that were found in association with a left mandibular ramus collected from King Island which they identified as *P. anak*. Efforts to relocate these bones in the collection of the Queen Victoria Museum (Launceston) have so far been unsuccessful (Tassell pers. comm.), but the fact that Scott and Lord made no mention of any peculiarities of form in these bones suggests that, like the Morwell humerus, they were essentially similar in form to, but much bigger than, those of a large extant species of *Macropus*.

Another large form which is not so far known from this site, but which occurs in other Pleistocene sites in south-eastern Australia is the vombatid *Phascolonus*. Greater size and the extreme development of ridges and crests (Stirling 1900, plate 49 (1); Murray 1991, fig. 17) distinguish the humerus of *Phascolonus* from the bone shown in Fig. 7.

Thus by a process of elimination *P. oscillans* appears to be the only large form presently known from (or likely to turn up in) Henschke's Fossil Cave that might have yielded a humerus of this type.

Support for this interpretation is provided by features which ally the humerus of Fig. 7 with the equivalent bone in *Hypsiprymnodon moschatus*. This positive evidence is now considered.

In comparison with the humeri of extant macropodiform (and most other) marsupials the outstanding feature of the Henschke's Cave humeri shown in Figs 7 and 8 is the very simple contouring of the shaft surface. As we shall see this is one of the features that the humerus of Fig. 7 shares with *H. moschatus*. However, it should be noted that it is bipedal members of the macropodiforms, rather than *H. moschatus*, that exhibit the 'standard' humeral morphology that obtains in generalized quadrupedal marsupials such as *Didelphis*, *Antechinus* and *Trichosurus* and in most bandicoots.

In the potoroids *Potorous tridactylus* (Figs 25G, 26G), *Aepyprymnus rufescens* (ANWC MAMS-9), *Bettongia penicillata* (Figs 25I, 25O), *B. lesueur* (Figs 25J, 26J), the macropodids *Dendrolagus bennettianus* (Figs 25E, 26E), *Petrogale penicillata* (ANWC CM 13571), *P. xanthopus* (Figs 25D, 26D), *Setonix brachyurus*, *Lagorchestes*, *Onychogalea* (Merrilees and Porter 1979 p. 90, p. 81, p. 85), *Wallabia bicolor* (ANU PL), *Macropus parma* (Figs 25C, 26C), *Macropus eugenii* (Merrilees and Porter 1979 p. 99), *Macropus rufogriseus* (ANU DBZ), *Macropus fuliginosus* (Merrilees and Porter 1979 p. 109), *Macropus giganteus* (Figs 25B, 26B), the pectoral ridge is a very pronounced feature of the anterior surface of the humeral shaft. However, this structure is quite weakly developed in both *H. moschatus* (Figs 25J, 26J) and the very small macrop-



oidid *Dorcopsulus vanheurni* (Figs 25F and 26F).

The humeri of *H. moschatus* and *D. vanheurni* are further distinguished from those of most other macropodiforms by weak development of the deltoid ridge (Fig. 25J, F). In *Hypsiprymnodon* a relatively low weakly developed ridge can be found on the antero-lateral margin of the proximal humerus (Fig. 25J). As in several other macropodiforms this continues distally and makes contact with the pectoral ridge producing an elongate triangular area on the anterior surface of the proximal humerus which was described by Heighway (1939 p. 16). (Note however, that Heighway uses the name deltoid crest to refer to the structure which we identify as the pectoral ridge.) In *Dorcopsulus* the deltoid ridge is less extensive, and for the most part even more weakly developed, although it rises to a sharp narrow crest about a quarter of the way down the lateral surface of the bone (Fig. 25F). The deltoid ridge can be traced some way beyond this crest distally, but not as far as the pectoral ridge so that *Dorcopsulus* has no triangular area on the front of the humerus. In most other macropodiform marsupials the deltoid ridge is a very obvious feature of the lateral or antero-lateral surface of the humerus. In the rat-kangaroos *Aepyprymnus rufescens* (ANWC MAMS-9), *Bettongia lesueur* (Fig. 25H) and *B. penicillata* (Fig. 25I), its conjunction with the pectoral ridge is associated with the formation of a large triangular-shaped and very strongly protruded crest which is evidently a more robust version of the triangular area found in *H. moschatus*. A somewhat similar situation seems to exist in *Petrogale* and *Dendrolagus* (Fig. 25D and E), but in most other macropodiform species, including *Potorous tridactylus* (Fig. 25G), the two ridges do not join to form a robust crest. As already noted the deltoid ridge is very poorly developed in the Henschke's Fossil Cave humerus of Fig. 7.

In the extinct sthenurine kangaroos the pectoral ridge is said by Wells and Tedford (1995) to be less well developed than in *M. giganteus* but longer, while in comparison with the latter form the deltoid crest is said to be relatively larger in *Sthenurus stirlingi* but relatively smaller in *S. tindalei* and *S. andersoni*. However, both structures are clearly better developed in sthenurines of all sizes than in *H. moschatus* or *D. vanheurni* (Wells and Tedford 1995, fig. 26a, f).

The superficial similarity in form of the humeri of *Hypsiprymnodon* and *Dorcopsulus* is somewhat surprising, but though the articular surface of the humeral head is essentially spheroidal in both forms, in *H. moschatus* it is quite clearly elongate antero-posteriorly (Fig. 27B), whereas in *D. vanheurni* it is slightly more elongate transversely (Fig. 27D). Proximally the margin of the pectoral ridge is wrapped mesially in *D. vanheurni* so that it partly obscures the bicipital groove. This feature is shared by a number of macropodids including *M. parma* (Fig. 27E), but is completely lacking in *H. moschatus* (Fig. 27B).

*D. vanheurni* and *H. moschatus* show a most interesting difference in humeral torsion. In *D. vanheurni*, the articular axis of the elbow joint lies nearly at right angles to a line passing antero-proximally through the humeral head and the proximal pectoral ridge-bicipital groove transition, so that humeral torsion measures around  $6^{\circ} - 7^{\circ}$  ( $n=2$ ). In *H. moschatus* these two lines of reference are not orthogonal but offset from this such that humeral torsion measurements vary between  $14^{\circ} - 24^{\circ}$  (mean =  $18.7^{\circ}$ ,  $n = 6$ ). One consequence of this is that in *H. moschatus* the lateral portion of the distal humerus is more cranially situated and its medial portion more caudally situated than in the macropodid. A strong backward curvature of the proximal part of the supinator crest which further distinguishes *H. moschatus* from *D. vanheurni* (and from other living macropodiforms) seems to be related to this torsional difference. Finally it can be noted that, relative to the condition in *D. vanheurni* (Fig. 25F), the capitulum of *H. moschatus* appears to be abbreviated laterally and the entepicondyle somewhat reduced in size (Fig. 25J).

The humerus of macropodiform marsupials generally shows obvious curvatures in both the parasagittal and transverse planes; the mesial surface being concave (Fig. 25), and the posterior surface being concave proximally and convex distally (Fig. 26). These

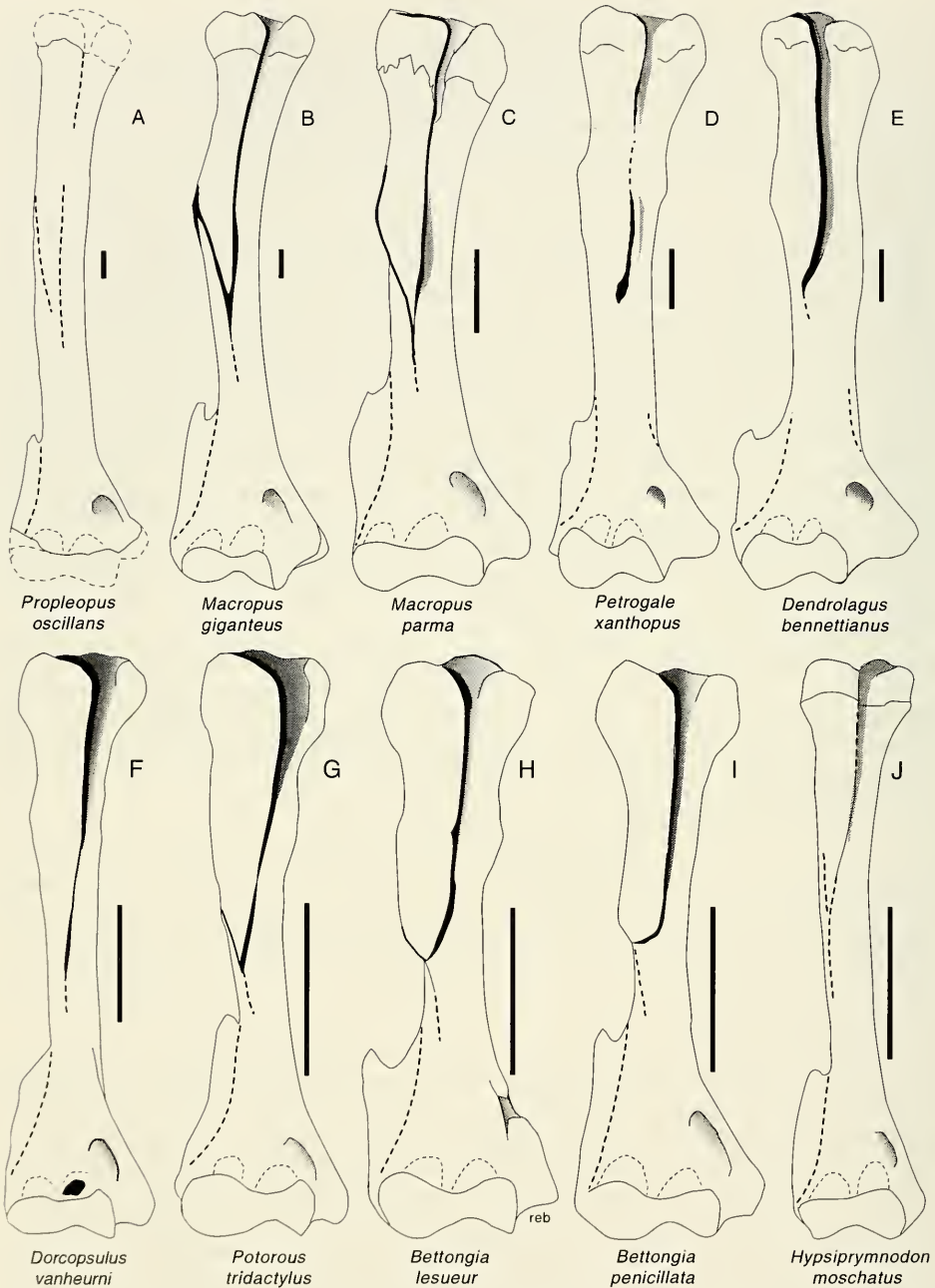


Figure 25. Right humeri of various macropodoid marsupials in anterior view. The illustrated humeri are from: A. Henschke's Fossil Cave specimen attributed to *P. oscillans* (P18846); B. *Macropus giganteus* (ANU PL); C. *M. parma* (ANU PL); D. *Petrogale xanthopus* (M11470); E. *Dendrolagus bennettianus* (M5530); F. *Dorcopsulus vanheurni* (ANWC CM15124); G. *Potorous tridactylus* (ANWC MAMS207); H. *Bettongia lesueur* (ANWC CM12873); I. *B. penicillata* (ANWC CM11458); J. *Hypsiprymnodon moschatus* (ANWC CM6051 and QM JM6187). The humeri have been brought to a common size to facilitate comparison. Scale bars = 10 mm. Epiphyseal reconstruction in A is based largely on the condition in *H. moschatus* (J).



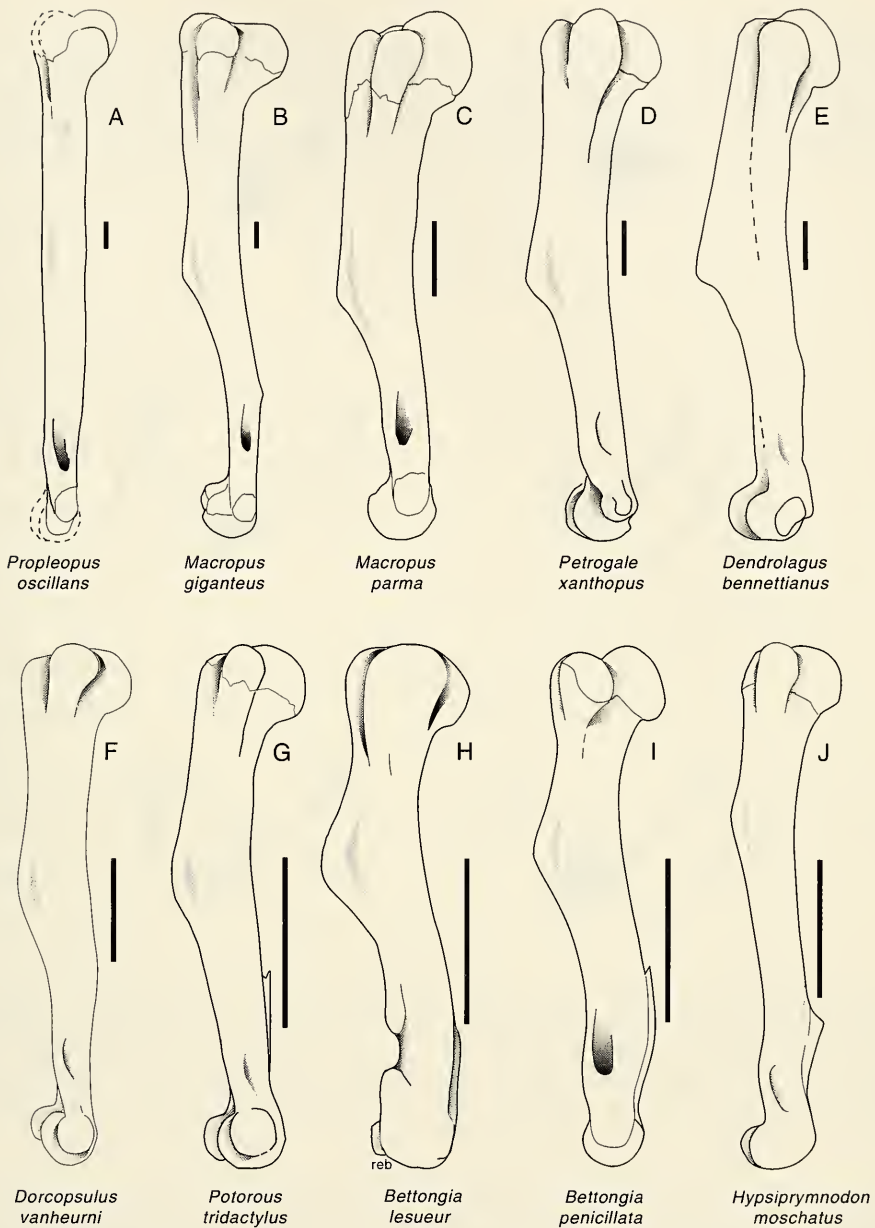


Figure 26. Right humeri of various macropodoid marsupials in medial view. The illustrated humeri are from: A. Henshke's Fossil Cave specimen attributed to *P. oscillans* (P18846); B. *Macropus giganteus* (ANU PL); C. *M. parma* (ANU PL); D. *Petrogale xanthopus* (M11470); E. *Dendrolagus bennettianus* (M5530); F. *Dorcopsulus vanheurni* (ANWC CM15124); G. *Potorous tridactylus* (ANWC MAMS207); H. *Bettongia lesueur* (ANWC CM12873); I. *B. penicillata* (ANWC CM11458); J. *Hypsiprymnodon moschatus* (ANWC CM 6051 and QM JM6187). The humeri have been brought to a common size to facilitate comparison. Scale bar = 10 mm. Epiphyseal reconstruction in A is based largely on the condition in *H. moschatus* (J).

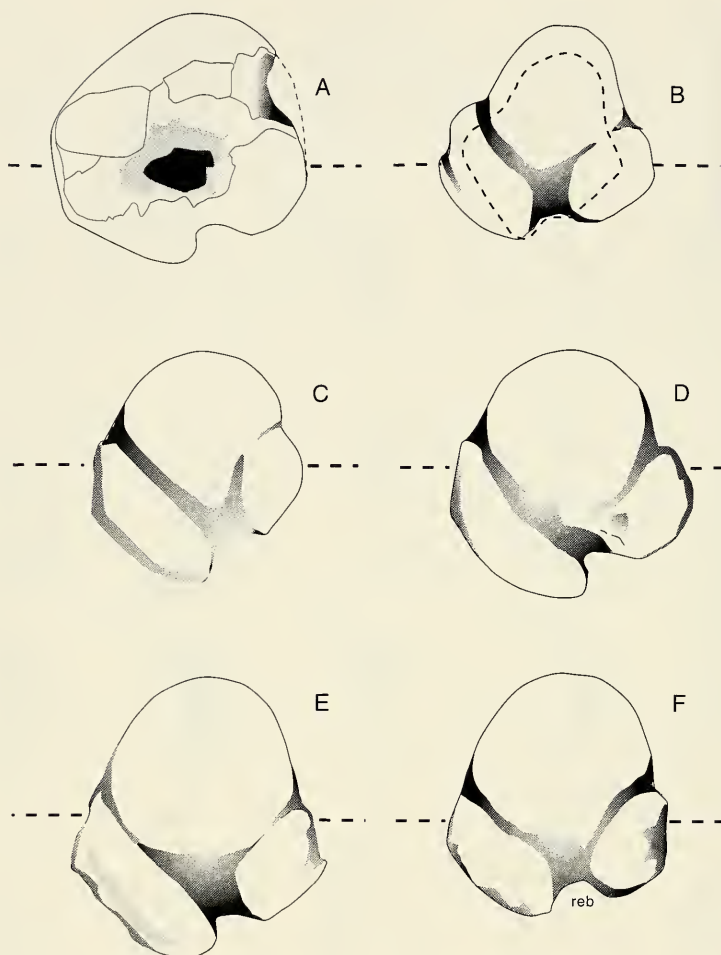


Figure 27. Proximal portions of the right humeri in end view of A. Henshke's Fossil Cave specimen attributed to *P. oscillans* (P18846); B. *Hypsiprymnodon moschatus* (QM JM 6187); C. *Potorous tridactylus* (ANWC MAMS207); D. *Dorcopsulus vanheurni* (ANWC CM15124); E. *Macropus parma* (ANU PL); F. *Macropus giganteus* (ANWC MAMS343). In each instance the bone is drawn with its anterior face directed towards the bottom of the figure and its posterior face towards the top. The approximate alignment of the articular axis of the elbow joint is indicated by a broken line. In B a broken line indicates the shape of a cross-section just below the head. The drawings have been brought to a common size to facilitate comparison.

curvatures are readily apparent in the humeri of large specimens of *Macropus giganteus*, with that in the transverse plane being more pronounced than that in the parasagittal one. All three curvatures are also evident in the humeri of the macropodids *Macropus parma* (Fig. 26C), *M. eugeni* (ANWC CM11450) and *Setonix* (ANWC MAMS 196) and, at least in the transverse plane, in *Onychogale* (Merrilees and Porter 1979 p. 85). In *Dendrolagus bennettianus* (Fig. 26E) and *Petrogale xanthopus* (Fig. 26D), there is no clear indication of curvature in the transverse plane and only slight evidence of it in the parasagittal one. The same would seem to be true of *Lagorchestes* (Merrilees and Porter 1979 p. 81). The three curvatures are evident in members of the genus *Sthenurus* (Wells and Tedford 1995, fig. 26).



TABLE 2

Humeral torsion in various marsupials. Extreme estimates are given for the single most complete humerus of *P. oscillans* and the real value undoubtedly lies within these. With the other species single estimates were obtained from each humerus. All values were obtained by placing the bone upright with the axis of rotation of the elbow joint set along a previously drawn line and then establishing a second line through the most posterior part of the articular surface of the humeral head and the proximal part of the lateral margin of the bicipital groove. The method is imprecise and may involve errors of up to 5 degrees; nevertheless, data trends are considered reliable. Where left and right humeri were available two values have been given.

Species	Number of humeri examined	Values
<i>Propleopus oscillans</i> (P18846)	1	12° – 27°
<i>Hypsiprymnodon moschatus</i> Qd Mus. JM6915	2	18°, 24°
<i>Hypsiprymnodon moschatus</i> Qd Mus. JM6187	2	16°, 20°
<i>Hypsiprymnodon moschatus</i> CM6051	2	14°, 20°
<i>Aepyprymnus rufescens</i>	2	2°, 2°
<i>Potorous tridactylus</i>	2	8°, 10°
<i>Bettongia penicillata</i>	2	4°, 9°
<i>Bettongia lesueur</i>	2	3°, 7°
<i>Dorcopsulus vanheurni</i>	2	6°, 7°
<i>Macropus parma</i>	1	6°
<i>Macropus giganteus</i>	1	10°
<i>Trichosurus vulpecula</i>	2	7°, 9°
<i>Phascolarctos cinereus</i>	2	2°, 4°
<i>Vombatus ursinus</i>	2	1°, 2°
<i>Thylacinus cynocephalus</i>	2	c. 2°
<i>Sminthopsis leucopus</i>	1	c. 13°
<i>Dasyurus maculatus</i>	2	7°, 10°
<i>Isodon macrourus</i>	2	3°, 7°
<i>Perameles</i> sp.	2	7°, 8°

Humeral curvature is weakly developed in the transverse plane in potoroids, but the double curvature of the sagittal plane is very evident in the humeri of the potoroids *Potorous tridactylus* (Fig. 26G), *Aepyprymnus rufescens* (ANWC MAMS-9), *Bettongia lesueur* (Fig. 26H) and *B. penicillata* (Fig. 26I). All three curvatures are relatively weakly developed in *Dorcopsulus vanheurni* (Figs 25F, 26F) and very weakly developed in *Hypsiprymnodon* (Figs 25J, 26J). As noted above, the Henschke's Fossil Cave humerus described by Pledge shows no evidence of proximal curvature and very little evidence of distal curvature in the parasagittal plane, while in the transverse plane it is moderately curved outward. The virtual absence of curvatures in the parasagittal plane is responsible for apparent straightness of this bone when viewed from a mesial or lateral perspective (Figs 7B, D, 25A, 26A).

Torsion measurements (Table 2) separate this bone and the humeri of *H. moschatus* from those of living potoroids and macropodids (including *Dorcopsulus*), and indeed from various quadrupedal marsupials as well. Whether such torsion is a feature of the humerus shared by all members of the Hypsiprymnodontidae remains to be established. As in *H. moschatus*, the proximal part of the supinator crest is turned caudally, although not so strongly as in the living form.

Overall P18846 is quite similar to the humeri of *H. moschatus* and *D. vanheurni*. All three humeral types share a simple form that is apomorphic among marsupials. However, when humeral torsion and other more subtle features of morphology are taken into account it is evident that P18846 and the humeri of *H. moschatus* share some derived features that are lacking in the humeri of *D. vanheurni*. This suggests that *H. moschatus* and the species from which P18846 came are closely related and, in conjunction with other evidence (see below), suggests that the simplified form of the humerus in these animals was acquired independently from that found in *D. vanheurni*.

In so far as the fossil humerus is essentially a scaled-up version of that of *H. moschatus* and in so far as features of cranial anatomy mentioned earlier in this study demonstrates that *Hypsiprymnodon* and *Propleopus* are morphologically similar forms, and since in our view they are quite closely related, we conclude that Pledge (1981) was right and that the humerus P18846 is attributable to *P. oscillans*. On the basis of its similarity to this bone we attribute the less complete, but larger, humerus, P35648 (Fig. 8), to *P. oscillans* as well.

The size of these humeri is not inconsistent with this attribution. The length of the skull of *P. oscillans* is some 3.6 to 3.7 times greater than that of *H. moschatus* whereas the presumed humeri are some 5.7 to 6.2 times larger than the equivalent element in *H. moschatus*. However, the skull tends to be proportionately smaller relative to the humerus in both large macropodoid (bipedal) and large dasyuroid (quadrupedal) marsupials than in small members of these groups, so that such differential scaling of skull and humerus is not unexpected.

### Humeral morphology and life style

The humerus alone provides a very limited basis for assessing life style in *P. oscillans*. Nevertheless, there are three lines of investigation that can provide some insight into the likely habits of the fossil form to the extent that these are reflected in humeral morphology. One involves comparison of the form of the humerus of *P. oscillans* with that of its nearest relative (i.e. *H. moschatus*). The second involves comparison of the form of this bone with the equivalent element in suites of mammals that represent particular habitus types (e.g. digging mammals, cursorial mammals, etc.). The third involves consideration of areas of muscle attachment on the humerus of *P. oscillans* and the inferences that can be drawn from these.

### Comparison of *P. oscillans* with *H. moschatus*

Recent studies of captive specimens of *H. moschatus* confirm that it is consistently quadrupedal (Johnson and Strahan 1982; Johnson pers. comm.), as reported earlier by Le Soeuf and Burrell (1926 p. 238) who noted that *H. moschatus* 'proceeds on all four feet like a rat'. Such behaviour sets *H. moschatus* apart from all living potoroid and macropodid marsupials which usually move quadrupedally at low speeds (this may not be true of forest wallabies), but are invariably bipedal at moderate to high speeds (Frith and Calaby 1969; Windsor & Dagg 1971; Morton and Burton 1973; Buchmann and Guiler 1974; Maynes 1974; Lundie-Jenkins 1993).

The considerable morphological similarity of the humeri of *P. oscillans* and *H. moschatus* suggests that the extinct form was not greatly dissimilar in its locomotor behaviour to the smaller living one. This implies that *P. oscillans* was probably quadrupedal at all speeds during normal terrestrial locomotion.

Two further questions arise immediately from this. Firstly, what are the locomotor capabilities of *H. moschatus*? In particular how capable a runner is it? Secondly, was *P. oscillans* more or less capable in this respect than *H. moschatus*?

Despite recent observations, we are relatively ignorant of the performance capabilities of *H. moschatus*. We do not know, for example, how its top speed compares with that of *Aepyprymnus*, *Bettongia* or *Potorous*. When travelling at maximum speed is it faster or slower than these small bipedal potoroids? Neither do we have any appreciation as to whether its capabilities run to brief bouts of relatively high speed or are more attuned to extended bouts of running at a more moderate pace. Likewise, the capacity of *H. moschatus* for other forms of locomotion remains little known. Dennis and Johnson (1995) note that it occasionally climbs in low vegetation such as fallen trees or branches and Johnson (pers. comm.) reports that it climbs well on thick branches that are inclined at angles of up to 45°. In such climbing it uses not only the whorled pads of its feet, but also its narrow and recurved claws which are surprisingly sharp (Johnson pers. comm.).

There remains the question as to whether the capacity of *P. oscillans* for terrestrial locomotion was more or less than that of *H. moschatus*. Two features which seem to be relevant to assessing the relative terrestrial locomotor capabilities of *P. oscillans* are the greater straightness of the shaft of its humerus when viewed from a lateral perspective, and the even weaker development on this bone of various ridges and processes that are not strongly developed on the humerus of *H. moschatus*.

As noted below greater straightness of the humerus in the parasagittal plane is rather equivocal as it appears to be characteristic not only of cursorial animals but also of larger ones. Less equivocal is the weak development of ridges in *P. oscillans*. As noted below, humeral morphology is generally simplified in cursors. Thus the simpler morphology of its humerus suggests that *P. oscillans* was capable of running relatively faster and/or longer than *H. moschatus*.

### Comparison of *P. oscillans* with various habitus types

The relation between humeral form and life style is not well understood in mammals and in the absence of information on the more distal elements of the forelimb or other parts of the postcranium it is very difficult to advance positive views about the life style of *P. oscillans*. Given this, our aim has been to narrow the range of possible life styles of *P. oscillans* by ruling out certain broad habitus types. To achieve this the humerus of *P. oscillans* is compared with the equivalent elements in a range of other mammals.

#### Comparison with bipedal saltators:

The morphological features that distinguish the humerus of *P. oscillans* from those of bipedal potoroids and macropodids strongly suggests that the fossil form did not use its forelimbs in a manner comparable to that of any living bipedal macropodiform. As already noted the superficial similarities that exist between this bone in forest wallabies



of the genus *Dorcopsulus* on the one hand, and *H. moschatus* and *P. oscillans* on the other, occur in conjunction with several subtle but significant differences which indicate that the humerus has been modified for quite different roles in the two groups. Simplification of the humeral shaft presumably reflects alterations in the character of the forces that are applied to it by the attaching muscles and, as we shall see, such simplification is common to several groups of mammals that are locomotively specialized in quite divergent ways.

That we are dealing with a divergent specialization in *Dorcopsulus* is indicated not only by the differences in humeral morphology just alluded to, but additionally by the very different proportions of the fore and hindlimbs in *Dorcopsulus* and *Hypsiprymnodon*, and by the very different form of the scapula in these two genera. Relative to femoral length, the humerus in *Dorcopsulus* is very similar in length to that of *Setonix*. In both these forms the humerus is relatively longer than in *Aepyprymnus* and *Lagorchestes hirsutus*, but relatively shorter than in *Potorous tridactylus*. In *Hypsiprymnodon*, in contrast, the humerus is proportionately much longer than in any of these forms. Indeed, relative to the femur, humeral length in *H. moschatus* closely approaches that of some peramelids and vombatids, although from this perspective the bone of *H. moschatus* is still proportionately much shorter than in dasyurids (Pridmore unpub. data). The scapula of the *H. moschatus* is a long and relatively rectangular bone (Heighway 1939, fig. 5; Johnson and Strahan 1982, fig. 10) which is essentially similar in outline to the same element in *Potorous*, *Trichosurus*, *Sarcophilus* (Merrilees and Porter 1979) and *Caenolestes* (Osgood 1921). It lacks the sharp rise in the anterior border immediately adjacent to the scapular notch which is found in *Dorcopsulus* and in other forms with short fan or trapezoidal-shaped capulae, such as *Setonix* and members of the genus *Macropus* (Merrilees and Porter 1979).

We suspect that the form of the humerus in *Dorcopsulus* reflects minimal use by this form of quadrupedal locomotion. Slow quadrupedal crawling has obvious importance for forms that grub amongst soil or leaf litter for food (most potoroids), and for forms that browse or graze on low growing leaves (most macropodids). However, it is likely to be of little use to small very manoeuvrable forms which obtain leaves that are growing well above ground. For an animal that has to extend its head upwards to grasp food items, the ability to use the bent tail as a third support (supplementary to the hindlimbs) would seem to be of far greater value than any capacity it might possess for supporting itself on its short forelimbs. George (pers. comm.) indicates that specimens of *Dorcopsulus* rarely, if ever, use quadrupedal locomotion. This suggests that the primary roles of the forelimbs in forest wallabies may have been reduced to manipulation of food at the mouth (Menzies 1991 p. 111), to use in toilet and to use in pouch manipulation.

Whether our interpretation is correct or not, the view of Lord and Scott (1924, p. 244) that the essential similarity of the humerus of *Macropus* to that of other marsupials is due to 'the urgent need for the manipulation of the pouch', would seem to be untenable since the pouch is well developed in both *Dorcopsulus* and *Hypsiprymnodon* (Menzies 1991; Dennis and Johnson 1995; Johnson pers. comm.).

Differences between the humeri of *P. oscillans* and *H. moschatus*, on the one hand, and those of other macropodiform marsupials, on the other, are evident in radiographs. These show the shaft of the humerus of *P. oscillans* to be supported by a dense cortical layer of bone which extends along almost the entire length of the diaphysis on all sides (Figs 29A, 30A). A similar situation is found in *H. moschatus* (Figs 29B, 30B), although the cortical layer is markedly less developed in the smaller form. Extended cortical thickening does not characterize the entirety of the humeral shaft in potoroid or macropodid marsupials, including *Dorcopsulus*. In these forms dense cortical bone is found on the posterior, mesial and lateral surfaces of the shaft, but not on the anterior surface, at least proximally (Figs 29C-I, 30C-I). The same is true of the phalangerid *Trichosurus* (Figs 31A, 32A).

Comparison with digging, swimming and typical climbing mammals:

The relatively straight form and smooth surface of the humeral shaft in *P. oscillans* would seem to exclude from consideration life styles in which much time was spent in digging, swimming or climbing in trees in the usual mammalian quadrupedal manner. In mammals that habitually undertake such activities, the deltoid crest is developed to a much greater extent than in *P. oscillans*. However, the ridges of the humeral shaft are weakly developed in certain atypical types of arboreal mammals, in cursorial mammals and in some ambulatory mammals.

Comparison with certain atypical arboreal mammals:

To some extent the condition of the humerus of *P. oscillans* is approached in the vertical-clinging-and-leaping lemuroid primate *Indri*. In this form the shaft of the humerus is akin to a simple cylinder and except for a small anterior crest is largely free of significant protuberances over its length (Vallois 1955, fig. 1860). However, the humerus of *Indri* is at once both too gracile and equipped with too large an anterior crest (see Hill 1953, plate 30) to serve as a credible model for *P. oscillans*. Moreover, to the extent that *Indri* and its relatives exhibit any transverse curvature, it involves lateral concaveness (Demes et al. 1991, fig. 3); exactly the reverse of the situation in *P. oscillans*.

Humeri that are superficially similar to that of *P. oscillans* are encountered also in those primates that habitually use an upright posture. These animals are sometimes termed brachiators, semibrachiators and modified brachiators (e.g. Napier and Napier 1967), but as Andrews and Groves (1975) have pointed out what they share is use of an upright posture and a tendency to employ their mobile forelimbs to reach widely during feeding. These primates which belong to several different lineages, all have straight cylindrical humeri in which the shafts are devoid of all but the most minute protuberances. Humeri of this type are also found in humans.

When compared with the humeri of other primates, those of forms that are upright-postured are characterized by changes in the relative size and position of the humeral head and of the adjacent pair of tuberosities. In the upright-postured forms the head of the humerus is spheroidal rather than ovoid and very much larger relative to the diameter of the shaft than in forms that rarely use an upright posture (Fig. 28A, B). In the former the head is centrally placed at the proximal terminus of the bone, whereas in the latter it is terminal but somewhat offset from the long axis so that it projects posteriorly as well as terminally. In forms that rarely use an upright posture, one of the tuberosities is often sufficiently large to project above the summit of the humeral head (e.g. *Papio* – Swindler and Wood 1973, plate 15), whereas the relatively smaller tuberosities of those that habitually use such a posture do not project above the summit of the head at any point (e.g. *Ateles* – Figs 31E, 32E; *Hylobates* – Giebel and Leche 1874-1900, plate 81; *Pan* – Figs 31F, 32F). Another difference concerns the bicipital groove, which is narrow and sometimes partly closed in members of the former group (Fig. 28B), but broad and quite open in members of the group that do not habitually use an upright posture (Fig. 28A). Moreover, there is a tendency for the lesser tuberosity to atrophy in forms that commonly use an upright posture (Fig. 28B), whereas the proximal tuberosities are generally subequal in size in forms that rarely use an upright posture (Fig. 28A).

Several of these features of the proximal humerus of upright-postured primates are shared by sloths (Miller 1935, fig. 1; Beddard 1958, fig. 98; DeBlase and Martin 1981, fig. 8.15). Like gibbons and spider monkeys, sloths use their forelimbs as suspensory supports. Unlike gibbons, they obtain support in suspension from their hind as well as their forelimbs. In the three-toed sloth *Bradypus* the globular head, which is similar in diameter to the humeral shaft, is sited terminally on the axis of the bone and projects well above the proximal humeral tuberosities (Lessertisseur and Saban 1967, fig. 524A). In this form also, the lesser tuberosity is considerably smaller than the greater and very much smaller than the humeral head (Fig. 26C). In a specimen of the two-toed sloth

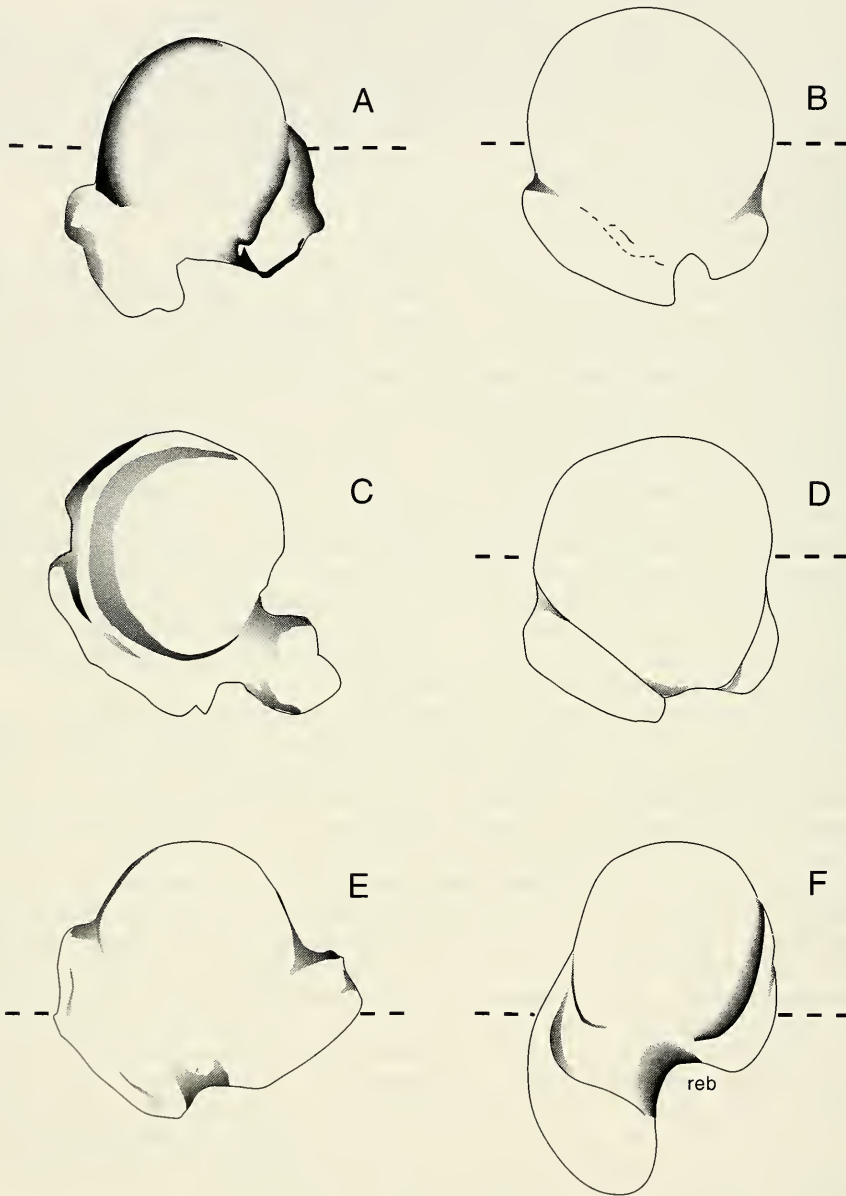


Figure 28. Proximal portions of the right humeri in end view from: A. baboon *Papio*; B. spider monkey *Ateles* sp.; C. three-toed sloth *Bradypus*; D. opossum *Didelphis* sp.; E. brushtail possum *Trichosurus* (ANU PL); F. thylacine *Thylacinus* (NMA IAC). In each instance the bone is drawn with its anterior face directed towards the bottom of the figure and its posterior face towards the top. The approximate alignment of the articular axis of the elbow joint is indicated by a horizontal broken line. The diagram of *Papio* is based on plate 15 of Swindler and Wood (1973), that of *Bradypus* on plate 76 (7a) in Giebel and Leche (1874-1900) and that of *Didelphis* on fig. 5 of Evans and Krahle (1945). The other three are original. The drawings have been brought to a common size to facilitate comparison.



*Choloepus* which we have examined, the humeral head is terminal but directed dorsally as well as terminally. It projects well above the proximal tuberosities and has a somewhat greater diameter than the shaft of the bone. However, the proximal tuberosities are more equally developed than in *Bradypus*. As in the humerus of *P. oscillans* the pectoral and deltoid ridges are very weakly expressed and the entepicondylar foramen well developed. However, the humerus of *Choloepus* which exhibits no obvious curvature in the transverse plane, exhibits obvious dual curvature in the parasagittal plane (Fig. 32G) and has a rather well developed supinator crest (Fig. 31G).

While the humerus of *P. oscillans* exhibits some similarity to those of upright-postured primates and of sloths, it is much less gracile than the equivalent element in these forms. This more stout configuration and the obvious curvature of the humerus in the transverse plane argue against the forelimbs of *P. oscillans* having served in a similar fashion to those of these non-marsupials.

Further evidence against such use is provided by radiographs. Although extended cortical thickening of the humeral shaft is evident also in the primates *Ateles* and *Pan* (Figs 31E, F, 32E, F), relative to humeral length, cortical bone is proportionately much thicker in *P. oscillans* than in the two primates. Moreover, whereas cortical bone is somewhat more thickly developed on the mesial surface of the humeral shaft in *P. oscillans*, the reverse seems to be the case with *Pan* and the sloth.

#### Comparison with quadrupedal cursorial mammals:

Quadrupedal cursorial adaptations are widespread amongst the Mammalia and mammals that travel far and/or fast share a suite of postcranial characteristics that generally includes a humerus in which the shaft appears largely free of bony protuberances. Indeed, in most cursors the humeral shaft has the form of a tapered ovoid cylinder. It should be noted, however, that the apparent absence of protuberances is a feature which shows some tendency to disappear at large body size. Thus while the humeral shaft seems to have been relatively smooth in the Eocene equid *Hyracotherium* (est. 24 to 35 kg) and to have carried a small deltoid crest in both the Oligocene form *Meshippus* (est. 42 to 48 kg) and the Miocene form *Merychippus* (est. 85 to 101 kg) (Simpson 1951; MacFadden 1986), this configuration no longer obtains in the modern riding horse (c. 200 kg). In such forms of *Equus caballus* the deltoid crest is very robustly developed (Smythe and Goody 1975, fig. 13).

The weight of *P. oscillans* is unknown, but several authors have suggested that the animal was similar in size to a modern red or gray kangaroo of similar mandibular length (e.g. Woods 1960; Pledge 1981; Archer et al. 1991). Flannery (1985 p. 245, 1989 p. 17) has estimated that the weight of *P. oscillans* was close to 70 kg. These estimates of size and weight are based on analogy with large bipedal macropodids. However, given that *P. oscillans* was most probably quadrupedal, an estimate of weight can also be obtained by using regression equations that relate humeral length to body weight in a large size range of quadrupedal placental mammals (Alexander et al. 1979). Of the four equations relating humeral length and body weight obtained by Alexander et al., that which best fits data for *H. moschatus* is the one that uses values for all placental mammals. Substituting a length of 210 mm into this equation yields a body weight estimate for *P. oscillans* of 51 kg with 95% confidence limits of 34 and 78 kg. The 210 mm long bone lacks epiphyses and so is probably from a sub-adult animal, which suggests that this is likely to be an underestimate of adult weight in *P. oscillans*. Taking this into account an adult weight similar to that estimated by Flannery (1985, 1989) is suggested. Evidently, *P. oscillans* exceeded in weight, not only the dingo, but also *Thylacinus cynocephalus* (15 – 35 kg) (Rounsevell and Mooney 1995).

From a lateral perspective the humeri of most mammals appear sigmoid (Fig. 32B-D). A larger curve, involving concaveness of the anterior surface, occupies the proximal two thirds or so of the bone and the smaller concave-posterior curve uses the remainder.

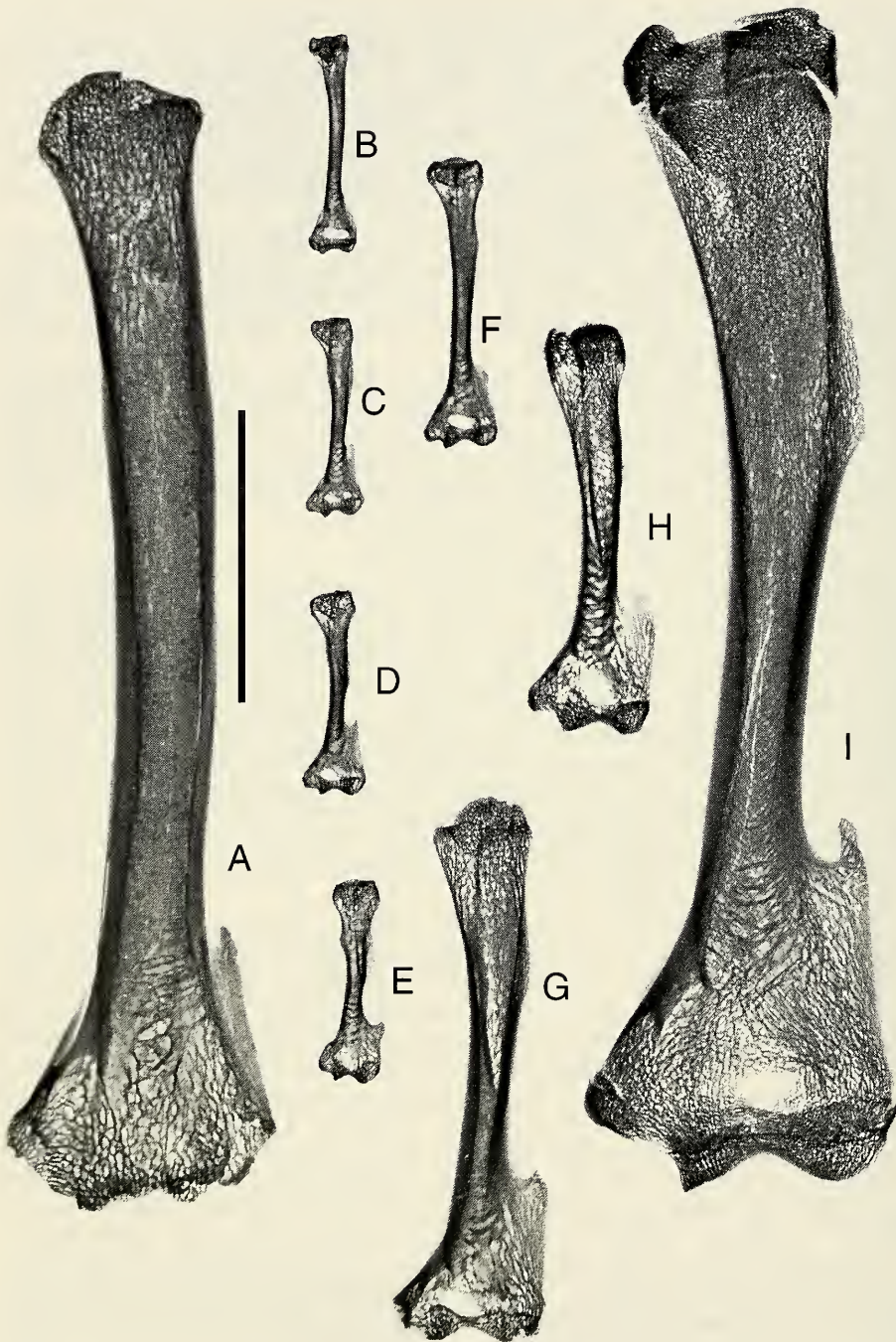


Figure 29. Antero-posterior projection radiographs of right humeri from: A. Putative *P. oscillans* (lacking proximal and distal epiphyses); B. *Hypsiprymnodon moschatus*; C. *Potorous tridactylus*; D. *Bettongia penicillata*; E. *B. lesueur*; F. *Dorcopsulus vanheurni*; G. *Wallabia bicolor* (lacking proximal epiphysis); H. *Macropus parma*; I. *Macropus giganteus*. Note that due to image reversal mesial is to the left. Scale bar = 5 cm



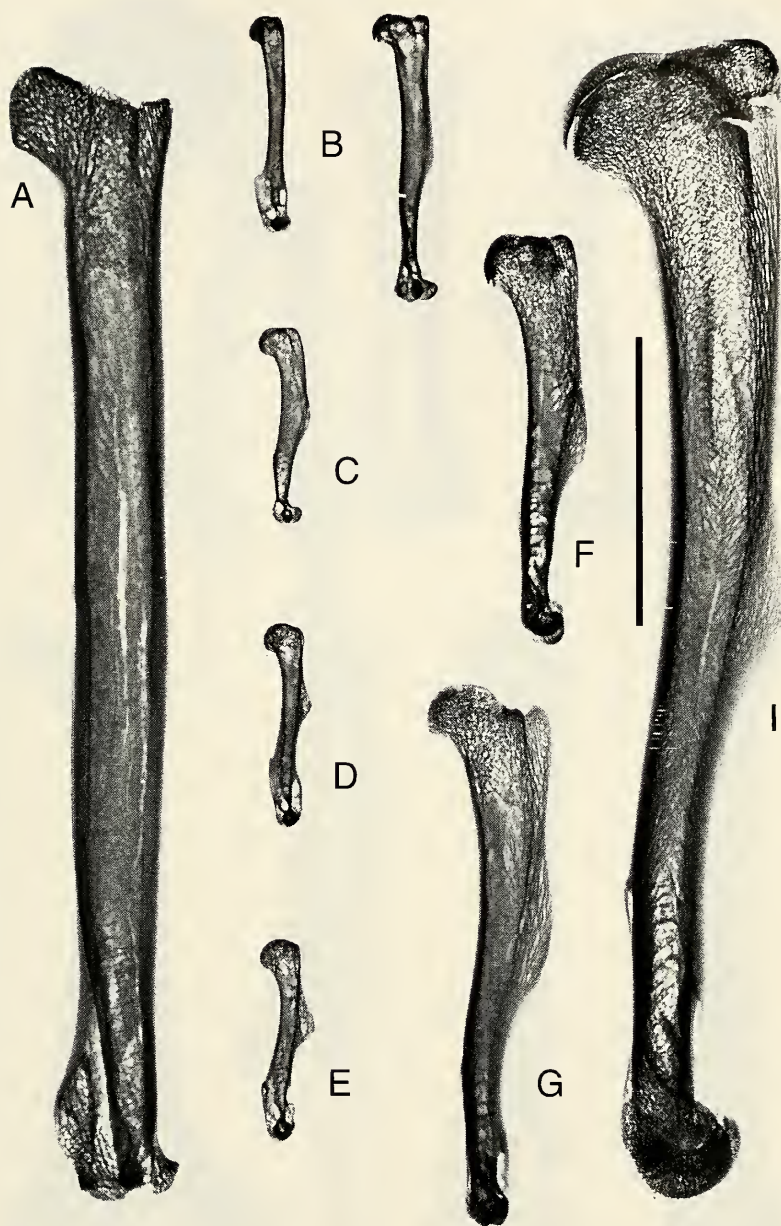


Figure 30. Transverse projection radiographs of right humeri from: A. Putative *P. oscillans* (lacking proximal and distal epiphyses); B. *Hypsiprymnodon moschatus*; C. *Potorous tridactylus*; D. *Bettongia penicillata*; E. *B. lesueur*; F. *Dorcopsulus vanheurni*; G. *Wallabia bicolor* (lacking proximal epiphysis); H. *Macropus parma*; I. *Macropus giganteus*. Scale bar = 5 cm.



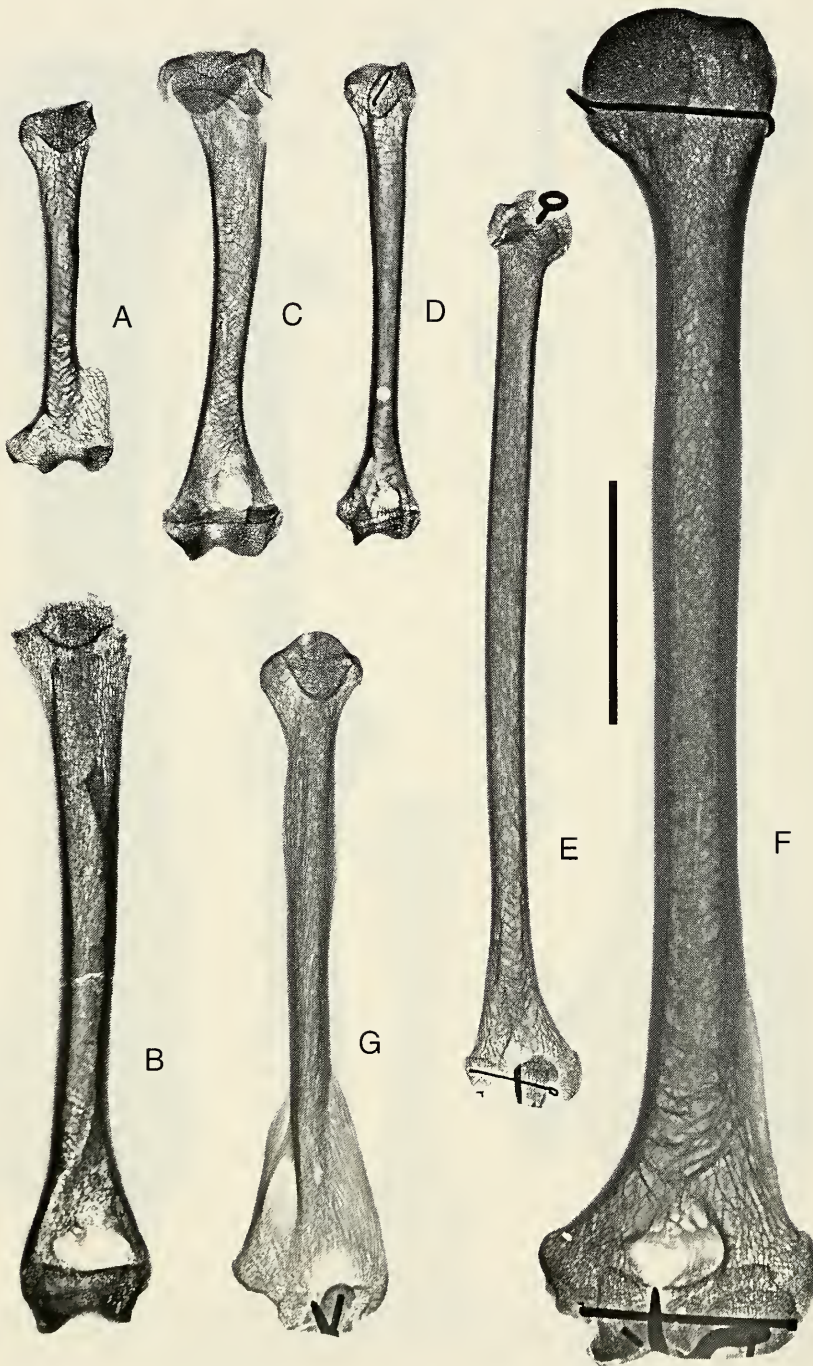


Figure 31. Antero-posterior projection radiographs of humeri from: A. *Trichosurus vulpecula*; B. *Thylacinus cynocephalus* (NMA IAC)(proximal portion lacking); C. *Canis familiaris* (ANU PL); D. *Felis catus* (ANU PL); E. *Ateles* sp. (NMA IAC); F. *Pan troglodytes* (NMA IAC); G. *Choloepus* sp. (NMA IAC). All are right humeri except E. Note that due to image reversal mesial is to the left in all but E. Scale bar = 5 cm.



Figure 32. Transverse projection radiographs of humeri from: A. *Trichosurus vulpecula*; B. *Thylacinus cynocephalus* (proximal portion lacking); C. *Canis familiaris*; D. *Felis catus*; E. *Ateles* sp.; F. *Pan troglodytes*; G. *Choloepus* sp. All are right humeri except E. Scale bar = 5 cm.



This dual curvature in the parasagittal plane seems to be affected by body size; data on humeri from a variety of ungulates, carnivorans and rodents indicate that curvature in the parasagittal plane tends to reduce with increasing body size (Biewener 1983, fig. 6). It appears to be influenced by locomotor habits as well; examination of the data provided by Biewener reveals that all of the forms in which curvature is relatively slight are ground-dwellers and that most are at least moderately cursorial. Support for the view that reduced curvature is a feature of cursors is provided by Hopwood's drawings (Hopwood 1947, fig. 2) of the humeri of lion, leopard and cheetah. These indicate that the humerus of the cheetah is less curved in the parasagittal plane than are those of the lion or leopard, despite the greater body weight of the latter two species.

Unfortunately, because of the great difference in size of *P. oscillans* and *H. moschatus*, it is impossible to tell whether the greater straightness of the humerus of the fossil form is due solely to greater size, or whether it also reflects greater running ability.

Viewed from an anterior or posterior perspective the humeri of cursors are straight or very slightly curved (Fig. 31B-D). Curvature in the transverse plane is lacking in *Felis catus* (Fig. 31D), *Acinonyx jubatus* (Van Valkenburgh, Grady and Kurten 1990, fig. 5) and in *Equus* (Smythe and Goody 1975, fig. 13) and *Rhinoceros* (Lessertisseur and Saban 1967, fig. 529). Its absence in these last two cursorial forms would seem not to be attributable to size since curvature in the transverse plane is evident in the larger ambulator *Elephas* (Lessertisseur and Saban 1967, fig. 529). However, the humerus is weakly bowed (concave medially) in *Canis* (Fig. 31B), *Crocuta* (Giebel and Leche 1874-1900, plate 79 (5) and *Thylacinus* (Fig. 31C). Thus, if *P. oscillans* was a cursor, the bowing of its humerus which is evident from an anterior or posterior perspective (Fig. 7A, C), would seem to place it with endurance cursors of the canid-hyaenid type rather than with sprint cursors of the felid type.

As in *P. oscillans* extended cortical thickening of the humeral shaft is evident in *Thylacinus* (Figs 31B, 32B) and in various placental cursors (Figs 31C, D, 32C, D) and, relative to humeral length, the cortical bone in all these forms appears to be of proportionately similar thickness. Moreover, in both *P. oscillans* and these cursors cortical bone is somewhat more thickly developed on the mesial wall of the humeral shaft.

At midshaft the humerus of *P. oscillans* is ovoid in cross-section; the transverse dimension of the bone being greater than the antero-posterior one. This is exactly the reverse of the situation in many living cursors in which the humerus is laterally compressed at midshaft (Table 3). It is unlikely that the broad condition of the humerus evident in *P. oscillans* is a heritage feature since the midshaft is laterally compressed in *H. moschatus* and in most other diprotodont marsupials (Table 3).

This evidently derived feature of the humerus of *P. oscillans* is not easily explained. Some transverse broadening is evident in *Thylacinus* (Table 3), but since we do not understand the significance of this it shines little light on the condition in the fossil form. Broadening suggests that the humerus of *P. oscillans* was more substantially loaded with transverse forces than is the case with the humeri of most mammals. Such loading could have been imposed during locomotion if the animal frequently changed direction. Alternatively, midshaft shape might reflect some other use of the forelimbs in *P. oscillans*; perhaps a role for the forelimbs in dealing with prey as Vickers-Rich and Rich (1993 p. 197) conjectured, although in the absence of distal limb elements this interpretation is as yet without real foundation.

#### Comparison with ambulatory mammals:

The general condition of the humeral shaft seen in *P. oscillans* is approached to some extent in a few relatively slow moving terrestrial (or largely terrestrial) mammals of medium size. These medium-sized ambulators include *Erinaceus*, *Erithizon*, *Procyon*, *Mephites* and *Sarcophilus*. They lack the capacity for fast running (Garland 1983) and avoid predators either through use of a defensive covering of spines or quills (*Erinaceus*



TABLE 3

Ratio of medio-lateral to antero-posterior dimension of humerus at midshaft in *P. oscillans*, *H. moschatus* and in various cursorial (c) and other quadrupedal mammals. The values Hopwood (1947) were taken at the level of the deltoid tuberosity (i.e. slightly more proximally than values collected in the present study).

Species	Number of humeri examined	Mean ratio	Source
<i>Propleopus oscillans</i> (P18846)	1	1.09	this study
<i>Propleopus oscillans</i> (P35648)	1	>1.00	this study
<i>Hypsiprymnodon moschatus</i> Qld Mus. JM 6187	2	0.74	this study
<i>Hypsiprymnodon moschatus</i> Qld Mus. JM 6915	2	0.69	this study
<i>Antechinomys laniger</i> (c)	1	0.67	this study
<i>Sminthopsis leucopus</i>	2	0.72	this study
<i>Dasyurus maculatus</i> M6187	2	0.66	this study
<i>Dasyurus maculatus</i> M2085	2	0.72	this study
<i>Sacrophilus harrisii</i>	2	0.65	this study
<i>Sacrophilus harrisii</i>	1	0.86	this study
<i>Thlacinus cynocephalus</i> M1960 (c)	2	0.83	this study
<i>Thlacinus cynocephalus</i> M5245 (c)	2	0.82	this study
<i>Isoodon macrourus</i>	1	0.48	this study
<i>Perameles</i> sp.	1	0.54	this study
<i>Chaeropus ecaudatus</i> (c)	1	0.70	this study
<i>Lasiiorhinus latifrons</i>	2	0.93	this study
<i>Trichosurus vulpecula</i>	1	0.84	this study
<i>Gulo gulo</i> 1	2	0.74	this study
<i>Gulo gulo</i> 2	2	0.85	this study
<i>Felis catus</i> (c)	1	0.81	this study
<i>Panthera pardus</i> (c)	?	0.75	Hopwood (1947)
<i>Panthera leo</i> (c)	?	0.70	Hopwood (1947)
<i>Acinonyx jubata</i> (c)	?	0.57	Hopwood (1947)
<i>Cabis familiaris</i> (c)	1	0.80	this study
<i>Equus caballus</i> 1 (c)	1	0.82	this study
<i>Equus caballus</i> 2 (draught)	1	0.78	this study

and *Erithizon*), threats and climbing ability (*Procyon* and *Sarcophilus*), or the release of noxious odours (*Mephites*).

In *Erinaceus* the humerus is a stocky bone, quite out of proportion to the equivalent element in *P. oscillans* (Lessertisseur and Saban 1967, fig. 529L; Gregory 1910, fig. 27.16). In *Procyon* the humerus is a relatively straight bone which shows little evidence of curvature in the transverse plane. It appears to be quite weakly ridged anteriorly (Giebel and Leche 1874-1900, plate 78 (6, 7)), although without a specimen to hand this cannot be confirmed. In *Sarcophilus* (ANU PL) the humerus is relatively straight in anterior or posterior view, but unlike the equivalent bone in *P. oscillans*, is clearly sigmoid when viewed laterally. The surface contours of the shaft are generally simple although there is a moderately developed deltoid ridge. Other features which distinguish the humerus of *Sarcophilus* from that of *P. oscillans* include moderately strong development of the greater tuberosity, 'lateral compression' of the shaft at midlength (Table 3), and negligible development of the supinator crest. In general, the form of the humerus in all these animals, to the extent that we have been able to investigate it, suggests that they do not provide a good model for *P. oscillans*.

The wolverine, *Gulo gulo* is in some respects intermediate to cursors and ambulators. Available accounts provide no indication that *Gulo* is capable of rapid running. On the other hand, it possesses very considerable ability as an endurance runner. Its usual running gait is described as a loping gallop (Nowak and Paradiso 1983 p. 1004) and, according to Stroganov (1969), it can maintain this for 10-15 km without stopping. In posterior view the humerus of *Gulo* is slightly concave mesially and its shaft is without obvious posterior protuberances (Giebel and Leche 1874-1900, plate 79 (1), UWZS 21655, 21897). From a lateral perspective it is clearly sigmoid. Its anterior surface bears weakly developed pectoral and deltoid ridges; these are more evident on the humeri of the larger male specimen (UWZS 21655) than in the adult female (UWZS 21897), but still far from robust in the former. Contrary to the condition in *Canis*, *Felis*, *Thylacinus* (Fig. 28F) and *Sarcophilus*, the greater tuberosity is weakly developed and extends very little cranially of the anterior face of the bone. Medially there is an obvious teres tubercle about a third of the way down the bone. At mid-shaft the humerus of *Gulo* the antero-posterior dimension is slightly greater than the transverse one (Table 3). The supinator crest is similar in relative extent to that of *P. oscillans*. Thus, aside from its sigmoid curvature and laterally compressed cross-section at mid-shaft the humerus of *Gulo* appears to be a good analogue for the equivalent element in *P. oscillans*.

Overall morphological comparisons confirm that *H. moschatus* provides the best model for interpreting locomotion in *P. oscillans*. Additionally they reveal that, *H. moschatus* aside, the humerus of *P. oscillans* most resembles those of quadrupedal forms that are capable runners but of the slow endurance (*Gulo*) type rather than the fast sprint (*Acinonyx*) type. Thus, the assumption (Vickers-Rich and Rich 1993) that *Propleopus* was saltatorial (i.e. was a bipedal leaper like a kangaroo) appears to be wrong and the suggestion that it might have been a cheetah counterpart is, at least with regard to locomotor ability, very much called into question.

#### Muscles attaching to the humerus of *P. oscillans*

The task of comparing the development of humeral muscles in *P. oscillans* with those in forms belonging to all of the habitus types just considered is too a large task to be undertaken here. Some useful comparisons can be made, however, between certain muscles in *P. oscillans* and in *H. moschatus* and between the same muscles in the fossil and in extant potoroids and macropodids. Such comparisons provide some basis for independent assessment of the extent to which *P. oscillans* was likely to have been quadrupedal and cursorial.

It has long been held (Gregory 1912; Maynard Smith and Savage 1956; Hildebrand 1974, 1985) that the limbs of cursors differ from those of non-cursors in having muscles

more proximally inserted. This grows out of the view that faster movement of the distal limb can be achieved if the insertion of any limb muscle promoting such motion is moved closer to the joint about which this movement is occurring.

Following this line of argument we had initially sought to compare the location of particular areas of muscle insertion on the humerus of *P. oscillans* with the equivalent areas of insertion in *H. moschatus*. Our hope was that such comparisons would clarify the relative capabilities of the two forms. However, doubts arise about the utility of such comparisons because it is evident that the relative positions of insertion sites do not necessarily relate in a simple fashion to locomotor performance. Thus, although Hildebrand (1985a, p. 46) states that 'it is commonly recognized that many limb muscles of mammalian cursors do insert closer to the associated pivots than the same muscles of their less swift relatives', Howell (1944), in his review of specializations of the forelimb musculature for speedy quadrupedal progression, came to what would seem to be exactly the opposite conclusion. He asserted (op. cit., p. 94) that cursors show 'a tendency toward the distal migration of the insertion of certain muscles'. This apparent contradiction may be due to the fact that cursors do not always move at top speed, so that in all probability they possess what Maynard Smith and Savage (1956) and Hildebrand (1985a) call 'low gear' muscles as well as 'high gear' ones. However, the effects of loading on muscle performance further complicate the matter. As Hildebrand (1985a) notes, very high 'gear ratios' may not benefit cursors at all since by increasing the load that a muscle must bear they reduce both the muscle's rate of shortening and distance of shortening. Moreover, recent considerations of muscle architecture (Gans and deVree 1987; Gans 1988) suggest that many widely espoused views about the effects of varying muscle insertion may be overly simplistic.

Given this there would seem to be little to be gained at present from any comparison of the relative positioning of areas of insertion, per se, of humeral muscles in *P. oscillans* and *H. moschatus*.

Nevertheless, an examination of the areas of muscle insertion in *P. oscillans* is not without value. It is possible to compare the areas of insertion of a few muscles in *P. oscillans* with the equivalent areas in *H. moschatus* and other extant macropodiform marsupials, and by focusing on features related to the bone-tendon connection at these sites, rather than their position up and down the shaft, we can make some informative inferences about the relative development of the muscles concerned in *P. oscillans*.

Although some 20 or so muscles or muscle groups attach to the humerus in marsupials, only three seem amenable to this approach. These are the teres major and latissimus dorsi (together), and the supinator longus (= brachioradialis). Most other muscles are either too broadly attached for their sites of attachment to show clearly or too small and weakly attached for these sites to be recognised. A different problem arises with the deltoid musculature. The site of attachment of this muscle complex (the deltoid crest) is clear enough (Fig. 33), but examination of the literature suggests that there is no obvious relation between the size of the muscle complex and the deltoid crest in mammals.

#### Latissimus dorsi and teres major muscles

The latissimus dorsi and teres major are considered together here because in *H. moschatus* and *M. giganteus*, and indeed in many other mammals, they share a common insertion onto the mesial surface of the humerus. The former arises from the spines of the caudal thoracic vertebrae and lumbodorsal fascia and in some forms from the ribs as well. The teres major arises from the caudal angle of the scapula. The latissimus dorsi is much the larger muscle and because of its very important role in quadrupedal locomotion it is accorded most attention here.

Both the latissimus dorsi and teres major muscles act as humeral retractors (Walker 1980; Hopwood 1947; Howell 1944) and the importance of the former for rapid locomotion arises from its ability to propel the trunk forward and through the shoulder girdle; a



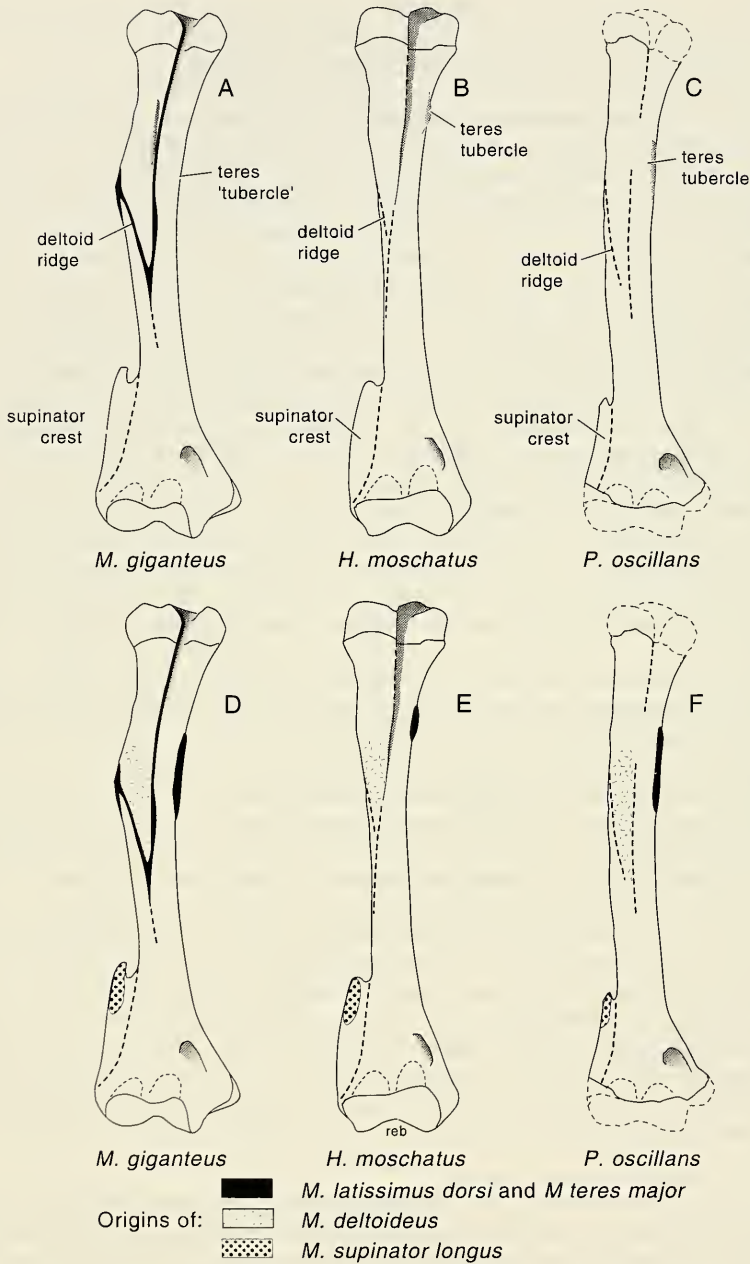


Figure 33. Anterior view of right humerus of A. *Macropus giganteus* (ANU PL); B. *H. moschatus* (based on ANWC CM6051 and QM JM6187); C. Putative *P. oscillans* (P18846). D, E and F; same humeri as in A, B and C, respectively, but with areas of origin and insertion of latissimus dorsi and teres major (together), and supinator longus muscles indicated. The sites of muscle attachment shown in D are based on Hopwood (1974). Those shown in E are based upon information given in Heighway (1939) and Carlsson (1915) and should be regarded as indicative rather than definitive. Those shown in F are inferred from C in conjunction with D and E.

capacity otherwise restricted to the posterior portion of the pectoralis muscle (Jenkins and Weijs 1979; Hopwood 1947). The latissimus dorsi is more strongly developed in the cheetah than in other felids, and is proportionately larger in *Canis lupus* and *Lycaon pictus* than in less cursorial canids (Gambaryan 1974, table 19). A similar, but more equivocal trend, is found in the teres major in these animals. In the cursorial antelopes *Procapra* (*Gazella*) *subgutturosa* and *Saiga tatarica* the latissimus dorsi is proportionately much larger than in the similar-sized but less cursorial chamois (*Rupicapra rupicapra*) (Gambaryan 1974, table 10). However, in hares (*Lepus* spp.) the latissimus dorsi is somewhat smaller than in the pika (*Ochotona alpina*) (Gambaryan 1974, table 25).

According to Heighway (1939) and Carlsson (1915) the common tendon of insertion of these two muscles in *H. moschatus* attaches into the bicipital groove (sulcus) of the humerus. The exact location of this attachment is not described by either author, but a small low ovate ridge is found about a quarter of the way down the mesial surface on several humeri available to us. We take this to be the site of insertion of the common tendon (Fig. 33B, E). In *M. giganteus* the site of insertion lies on the mesial or antero-mesial surface of the humerus about a third of the way down the bone (Fig. 33D; Hopwood 1974, fig. 17). In specimens of *M. giganteus* available to us this area is weakly pitted, but not marked by any local elevation or depression of the humeral surface.

In comparison with *M. giganteus* the common site of insertion of these two muscles (the so-called teres tubercle) is much more clearly marked in *P. oscillans*. In the fossil form a low ridge and a shallow groove extend in parallel down the mesial surface of the second quarter of the humerus (Figs 7A, B, 33C). The extent of the ridge cannot be determined with any precision but is estimated to be some 28–35 mm long in the fossil. Similar difficulty is experienced in determining the length of this tubercle in *H. moschatus*, but in the specimens available to us its length is around 2 to 5 mm.

Information is not available to allow us to establish unequivocally whether the development of the teres tubercle reflects the size of the muscles that insert onto it, although there are indications that this may be the case. A major problem in attempting to assess development of the latissimus dorsi concerns the extent to which the 'muscle' is fleshy as opposed to being made up of connective fascia. The teres tubercle is well developed in *Thylacinus* (NMA IAC), in various African antelopes (Hopwood 1936) and evidently also in the cheetah, the leopard and lion (Hopwood 1947). In *Thylacinus* the latissimus dorsi appears to be quite well developed (Cunningham 1882) and this muscle is certainly very well developed in the three carnivores just mentioned (Gambaryan 1974, table 19), but we are unable to assess whether this is true of the ungulate taxa. In *Trichosurus* (ANU PL) the tubercle rises very slightly above the surrounding bone. The latissimus dorsi of this form originates from the eight thoracic spines and caudal to this from a lumbar fascia. The muscle seems to be quite well developed in so far as the fleshy portion appears to extend quite far back along the dorsal surface of the trunk (Barbour 1963, fig. 21).

In *H. moschatus* the latissimus dorsi has a fairly extensive origin that takes in the spines of seven or eight thoracic vertebrae, the lumbar fascia and the last three ribs (Heighway 1939; Carlsson 1915). How much of the area of the muscle between these sites and its origin is fleshy and how much is connective fascia cannot be determined from the available accounts.

Amongst potoroids the teres tubercle is quite strongly developed in *Aepyprymnus* (CM MAMS 9) and *Bettongia lesueur* (CM 12873), both of which are habitual diggers, but more weakly developed in *B. penicillata* (CM 11458) and *Potorous tridactylus* (MAMS 207), which are not. We have no access to information on the development of the latissimus dorsi in any of these forms aside from the remark (Carlsson 1914) that in *Aepyprymnus* the muscle originates on five thoracic spines and several ribs and her observation that the origin is the same in *Petrogale*, but more extensive in both *Dendrolagus* and *Trichosurus*.

Amongst most macropodids both tubercle and muscle seem to be poorly developed. In *Macropus giganteus* the tubercle is, as previously noted, barely discernible, and the same is true of *M. rufogriseus* (ANU DBZ), *M. parma* (ANU PL), *W. bicolor* (ANU PL), *Petrogale penicillata* (ANWC CM13571) and *D. vanheurni* (ANWC CM 15124). The development of the latissimus dorsi seems not to have been described in any of these forms, although Boardman (1941) has given a good account of it in *M. robustus*. According to him the origin of the muscle is relatively lengthy and extends over the spines of ten thoracic vertebrae in this form. However, it is important to note that the proportion of the 'muscle' that is fleshy is relatively small and does not overlap onto the abdomen as is usually the case in mammals. In *Petrogale xanthopus*, in which the teres tubercle is moderately developed, the vertebral origin of the latissimus dorsi is less extensive; it arises from four or five thoracic spines, although contrary to the situation in *M. robustus* it also originates from (three) ribs (Parsons 1896; Carlsson 1915). In *Dendrolagus* the teres tubercle is also moderately developed and the origin of the latissimus dorsi extends over the spines of eight thoracic vertebrae and onto the ribs (Carlsson 1914; Boardman 1941). This presumably reflects the importance of the muscle in climbing.

It is evident that further studies are needed to establish whether the development of the teres tubercle does indeed reflect the size of the muscles that insert onto it. However, if it does, the relatively robust and elongate teres tubercle of *P. oscillans* would suggest that the latissimus dorsi was somewhat better developed in the fossil than in *H. moschatus* and considerably better developed than in living macropodids. A relatively larger latissimus dorsi muscle would be consistent with, amongst other things, slightly greater running ability in *P. oscillans* than in *H. moschatus*. While greater development of this muscle relative to the condition in *Macropus* would give strong support to the view that *P. oscillans* was habitually quadrupedal.

#### Supinator longus muscle:

The other muscle to be considered here is the supinator longus (= brachioradialis). This is one of a series of muscles associated with the supinator crest. It is the most proximally attaching of the muscles originating on this crest and inserts, in marsupials, onto the carpus. Cursorial forms generally exhibit reduced rotation of the forearm (pronation-supination) and reduced ability to manipulate the manual digits (Hildebrand 1974; Hopwood 1947) and these losses of capability are reflected in a reduction in size of the muscles that bring about such movements, including the supinator longus. Thus the supinator longus is absent in most ungulates (Windle and Parsons 1901), in rabbits (Walker 1980) and lacking also in the Patagonian cavy *Dolichotis* (Windle 1897). Amongst canids it is lacking in the cursors *Canis lupus* and *Lycaon pictus*, but present in the sub-cursorial Raccoon dog *Nyctereutes* (Gambaryan 1974, table 19). In most felids the supinator longus is present, but it is absent in the cheetah (Gambaryan 1974, table 19) and it is absent or vestigial amongst hyaenids (Windle and Parsons 1897).

The supinator longus is generally present in marsupials and the extent to which it is developed appears to be reflected in the size of the supinator crest from which it takes its origin. In *Sarcophilus* the muscle is lacking (Macalister 1872) and the bony crest is barely detectable (ANU PL). In *Thylacinus* the supinator crest is short and narrow (NMA IAC) and in accord with this the supinator longus is 'very feebly developed' (Cunningham 1882). In *Dasycercus* and *Trichosurus* both crest and muscle are reasonably well developed (Jones 1949; Barbour 1963) and in *Phascolarctos* both are developed to an extreme (Young 1882).

From this brief review it would seem to be the case that the acquisition of cursorial capabilities is generally associated in mammals with a reduction in size of the supinator longus muscle. Reduction may also occur in response to the adoption of other life styles (e.g. *Notoryctes*). Nevertheless, reduction of the supinator crest would seem to provide



good corroboration of cursoriality in forms where such capability is indicated by other morphological features.

According to Carlsson (1915) the supinator longus is well developed in *H. moschatus*; indeed comparably to the situation in *Trichosurus* and *Phalanger*. Heighway (1939) also indicates that the muscle is well developed in *H. moschatus*. This is not surprising given the relatively strong development of the supinator crest in this form (Fig. 25J).

In *Dendrolagus dorianus* the supinator longus is also strongly developed; Carlsson (1914) compares its development in this form with the situation in *Trichosurus* and notes that it has a broad origin on the supinator crest. According to her (op. cite) this muscle is very weakly developed in *Petrogale* in which form it has a less extensive origin on the humerus. Thus muscular development is reflected in the size of the supinator crest in these two genera (Fig. 25D, E).

There are few useful accounts of the supinator longus in other macropodiforms, but those that are available tend to confirm this correlation. Thus the muscle and bony crest appear to be moderately developed in *Macropus giganteus* (Hopwood 1974, fig. 4; Fig. 25B), while in *Aepyprymnus*, according to Carlsson (1914) the muscle has an especially broad origin, which is in good accord with the size of the bony crest in this form (ANWC MAMS-9).

In *P. oscillans* (Fig. 25A) the supinator crest is relatively smaller than in *H. moschatus* (Fig. 25J). This suggests that the supinator longus was reduced relative to the condition in *H. moschatus* (Fig. 33) and is consistent with the fossil form having been more cursorial than the living one. By the same token the reduction in size of this crest has proceeded to a far smaller degree than in *Thylacinus* (or even *Sarcophilus*) so that, unless the muscles of the supinator crest had some special non-running function (e.g. manipulation of food), it is difficult to believe that *P. oscillans* possessed more than semi-cursorial capabilities.

Development of the supinator crest in *P. oscillans* is obviously uninformative with respect to the question of whether the fossil form was habitually quadrupedal or partially bipedal.

Overall, what little we can infer about the development of muscles attaching to the humerus in *P. oscillans* is consistent it having been quadrupedal and having possessed some capability for running, although more appropriate for moderate speed endurance ability rather than any capacity for bouts of high speed locomotion as is sometimes implied.

## CONCLUSIONS

The hypothesis that *P. oscillans* was a carnivorous or omnivorous member of the Propleopinae can now be reviewed in the light of the additional material. As a consequence of being able to assess information from the dentition as part of a functioning masticatory complex, a number of alternative scenarios can be examined.

From our results, the following dietary life-styles open to mammals subsisting in the Australian arid and semi-arid zones, indicated by the distribution of *P. oscillans* fossils, can be eliminated:

Grazing and browsing – The incisors are unlike those of any grazing or browsing diprotodont mammal; in particular the reduction of  $I^{2-3}$  (as evidenced by their alveoli) indicates that they probably did not provide a flattened grasping platform for occlusion with the  $I_1$ . The sharpened beak-like  $I^1$  would not have been opposable for grasping and indicates a piercing function. In grazing diprotodonts, the  $I_1$ s are procumbent. The molar structure indicates that there was no expansion of the power stroke into Phase II. Molars

of *P. oscillans* are not lophodont or selenodont and give no evidence of capability for shearing-grinding a high fibrous diet. Grazing is excluded by absence of abrasion typical of phytolith inclusions in the diet and of adaptations to counter the wear produced by an abrasive diet (hypsodonty, dental progression). The masseteric complex is reduced as compared with the temporalis. The mandibular condyle is cylindrical rather than flattened and is placed at the level of the tooth row unlike any diprotodont herbivore.

**Rhizophagy** – On the basis of the above characters, as well as the absence of dental wear (both macroscopic and microwear features) that would indicate the presence of extensive grit from soil in the diet, rhizophagy can be excluded. The humerus also indicates that it was unlikely that the animal had fossorial capability.

**Frugivory and selective leaf-eating.** – While there is an apparent similarity to the molar morphology of leaf-eating monkeys (e.g. *Colobus guereza*), in the molars a major difference lies in the absence of structures in *P. oscillans* for the accommodation of the grinding phase (Phase II) of mastication used in mammals to disrupt plant fibres. Moreover, in all mammals in which there is extensive antero-mesial movement in the power stroke, the condyle is set high above the molar row (it is noteworthy that in the part-carnivorous baboon, *Papio*, the condyle is set much lower than in folivores). Frugivory (e.g. in *Ateles*) is also characterized by the presence of widened crushing molar facets and an extension of Phase II. Phase II of the masticatory cycle is matched dentally by the extensive development of transverse, complex shearing crests in diprotodont leaf-eaters (e.g. *Pseudocherius*, *Phascolarctos*) brought into use in the antero-mesial grinding stroke. Transverse shearing crests are of low relief in *P. oscillans*.

**Mycophagy** – The Potoroinae exemplify the mycophagous niche among diprotodont marsupials. All exhibit more extensive microwear than *P. oscillans*, almost certainly as a result of grit inclusions in the fungal diet. All have wear facets typical of mammals in which Phase II plays a significant part in the power stroke. The mandibular condyle is set above the molar row and the masticatory musculature does not have the temporalis large as compared with the masseteric complex, as in *P. oscillans* and Carnivora.

On the other hand, the morphological characteristics of *P. oscillans* do not deny the hypothesis that it was carnivorous.

### The structure of *P. oscillans*

The premolars and the molars, in themselves, confirm what was previously known of their structure and, as the result of more intensive examination (especially of the Cattle Creek specimen by scanning electron microscopy; Figs 9, 10, 13-18), the mode of their operation is now clear.

The premolars are shearing teeth which wear differentially in various parts of the teeth. Abrasion damage to the cusps is variable and there is no indication that these were used consistently for crack propagation in hard materials such as bone or the hard shells of fruit such as *Santalum*. The area of the premolar that is involved in direct tooth-on-tooth occlusion is small and is confined, certainly into full adult life, to the upper parts of the posterior ridges. Food material moved down the channels, but under less pressure than on the tops of the ridges. Some puncture crushing took place at the crest and its orientation is such as to indicate that the force was applied rearwards. The postero-lingual facet, which faces rearwards towards the first molar, exhibits crushing abrasion. In the both adult and juvenile dentitions abrasion in this part of the tooth indicates that it formed part of the shearing surface. This combination of features of the premolars of both adult and juvenile are consistent with the view that they were primarily used to shear tough material with hard inclusions of irregular size (some large enough to do considerable inadvertent damage). The appearance of these teeth is consistent with the shear-



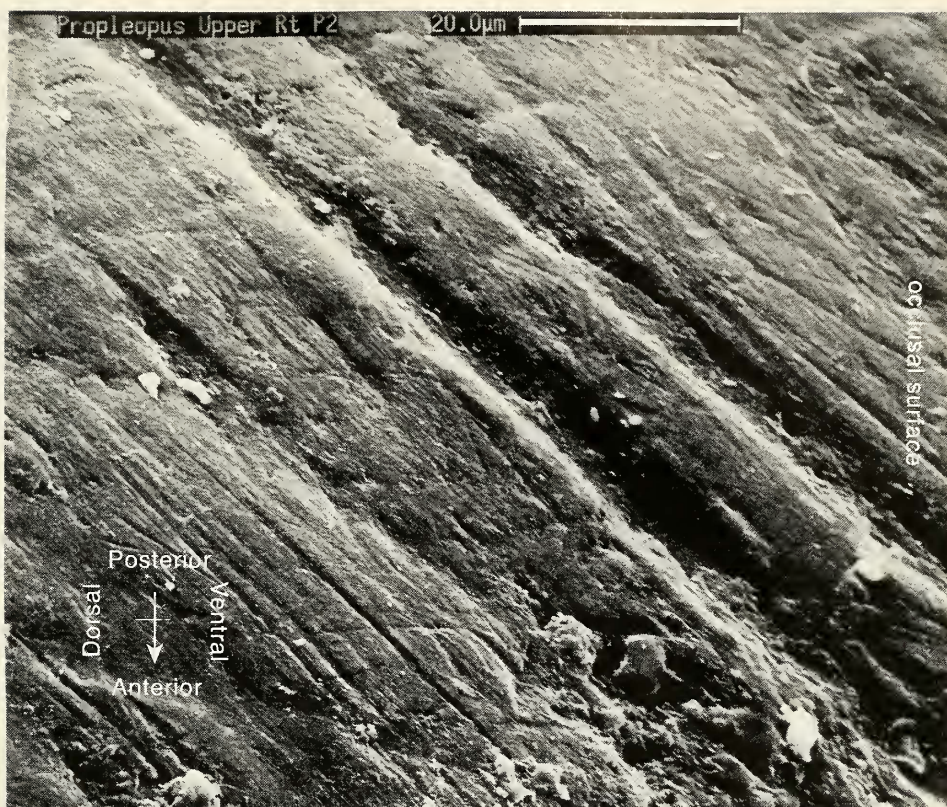


Figure 34. Abrasion grooving on the postero-lingual wear facet of  $P^2$  of *P. oscillans* (P24677). The variation in groove diameter and the presence of gouges illustrated is typical of carnivore carnassials (c.f. Van Valkenburgh, Teaford and Walker 1990, plate 1b, lion). Scale bar = 20  $\mu$ m.

ing surfaces of the carnassials of Carnivora. In the case of the Carnivora, the irregularity and considerable size of the inclusions is attributed to grit inclusions in hide and fragments of bone rather than to damage resulting from bone crushing.

The gross morphology of the molar row, supported by the microstructure of its abrasion features, indicates that when occluded, the outer rows of cusps (upper, buccal; lower, lingual) functioned as shearing elements with antero-postero ridges (cristae) bearing abrasion that indicates vertical or near-vertical shear. Damage to some cusps of these outer rows indicate that they may also have been inadvertently damaged by puncture-crushing. The inner rows of cusps that occlude within the median longitudinal valleys of their opposite partners are rounded, bearing abrasion features typical of elements used in crack propagation. The molar row does not diminish to any extent posteriorly indicating that both puncture crushing and shearing functions may have been applied locally or simultaneously over much of its length. Such tooth rows are found in *Thylacinus* and *Sarcophilus*<sup>10</sup>. *P. oscillans* differs from both in possessing a specialized shearing tooth in front; an inheritance from its diprotodont ancestry.

In conclusion, the morphology of its teeth, although atypical of any known living marsupial carnivore, are those that functionally fit an animal which fed on high energy foods (such as flesh) that did not require the grinding of tissues to break cell walls before they could be digested (as with plant tissues). In such a scenario, the primary food of *P.*



*oscillans* would have been one which required both piercing and holding, shearing, and crushing (both puncture crushing to propagate cracks through hard, brittle, inclusions, and crushing of soft tissues to separate structure (as in mechanical tenderizing)).

It is important to emphasize that the conclusions advanced here, although heavily influenced by dentition, do not depend upon dental morphology alone. The most significant new information (admittedly incomplete) derives from the cranial specimen. This indicates that *P. oscillans* was long faced; its premaxilla was strengthened in comparison with that of *H. moschatus*; the diastema was furnished with a canine that would have been useful as a holding device (but being without a functional opponent was probably not used to pierce); the molar row (with its dual crushing-shearing capability) was positioned forward in relation to the anterior root of the zygomatic; and the distance between the glenoid and masseteric process was shortened. The zygomatic arch was narrow but dorso-ventrally thick, especially above the middle of the molar row. The infraorbital foramen was large. By comparison with the mandible, the glenoid was located in approximately the palatal plane. In the upper jaw dentition, the first incisors were large and sharp and although succeeded by posterior incisors, these would have been small in height and probably did not share the piercing function of the anterior pair. The coronoid process of the mandible was wide antero-posteriorly (not slender or hooked) indicating a broad insertion of the temporal element of the adductor musculature. As in carnivores (but not herbivores or omnivores) the mandibular condyle was at the level of the molar row and was laterally elongate and cylindrical (the form of the glenoid is not known but with these features of the condyle it is anticipated that it would have had a strong post-glenoid process and have been open anteriorly).

Together, these features indicate an animal with a relatively long face and sensitive muzzle. It had the capacity to tightly grasp, pierce and hold. It had a wide gape and powerful vertically and posteriorly-acting masticatory muscles and a capacity to shear through and puncture crush tissue anywhere along the molar row. Its teeth give no indication that it ground its food.

Taken alone, the structure of the teeth may point in more than one direction. Thus, for example, a molar capable of Phase I crushing (as the molars of *P. oscillans* are) could certainly be used to crack nuts or crush fruit, but in a complex that points to hypertrophy of the temporalis, strengthened premaxilla, piercing and holding incisors, and cylindrical and low-set mandibular condyles, such a diet is unlikely to be primary. Moreover, if the arid and semi-arid Pleistocene was ecologically similar to the modern arid and semi-arid zones, it is likely that such foods could have formed part of the diet of an animal that was otherwise non-vegetarian. As a consequence, we consider that the data now point towards *P. oscillans* having been an opportunistic carnivore, i.e., a carnivore which, while being primarily carnivorous, was nevertheless capable of subsisting on a wide range of food materials. The diet of the fox (*Vulpes vulpes*: Carnivora) in arid Australia provides a modern example (Martensz 1971; Bayley 1978; Catling 1988).

The humeri attributed to *P. oscillans* are clearly distinguished from the humeri of bipedal macropodiform marsupials by the form and disposition of the pectoral and deltoid ridges and by degree of humeral torsion. In these and other features there is considerable similarity to the humerus of *H. moschatus*, which suggests that *P. oscillans* was, like the living form, quadrupedal at all speeds when travelling over-ground.

There are indications that the animal was somewhat more cursorial than *H. moschatus*, although since the relative running capabilities of the latter are not well understood, it is difficult to assess what this means relative to other forms. For a variety of reasons muscle insertion sites in *P. oscillans* are difficult to interpret. Nevertheless, the nature of the sites of insertion of the few humeral muscles that are amenable to assessment suggests that *P. oscillans* was less cursorial than *Canis* or *Thylacinus* and that it likely possessed capabilities for endurance rather than high speed running.

A peculiarity of the humerus of *P. oscillans* that distinguishes it from *H.*

*moschatus*, and other mammals, is its relatively broad cross-section at mid-shaft. This feature may be related to a role in prey capture (perhaps by ambush) or manipulation, but more distal limb elements are needed to assess this.

From a broader perspective this bone shows none of the characteristics evident in aquatic or semi-aquatic mammals, forelimb burrowers or arboreal forms that climb in trees in the quadrupedal mode adopted by most such mammals. Some similarities to the humeri of upright postured primates and sloths are evident, but these do not stand up to detailed comparison. Relative to the humeri of these forms the bone attributed to *P. oscillans* is less gracile, possesses a different distribution of cortical bone within the shaft and is distinguished also by curvature in the transverse plane. Greater similarities exist between the humerus attributed to *P. oscillans* and the humeri of quadrupedal cursors and fast ambulators. Of the forms we have been able to examine, it is the slow endurance cursor (or fast ambulator) *Gulo gulo* that most resembles *P. oscillans* in humeral form.

### ***Propleopus oscillans*: the animal**

All of these features contribute to an image of a wolf-sized animal that was primarily carnivorous, but probably a flesh-eater rather than a crusher of large bones (like, say, the large cats and *Thylacoleo*). In the arid and semi-arid environment it was probably a fox-like opportunist in its feeding habits. As we visualize it, *P. oscillans* would have been adept at capturing and consuming small to medium-sized vertebrate prey and scavenging on cadavers of larger animals. It would also have been equipped for opportunistic feeding such as on arthropods, fruits, etc. which the fox in arid Australia demonstrates can be so important to such a predator. It seems not to have been capable of rapidly running down large cursorial vertebrate prey, although it may have had some capacity for wearing down such forms through a slower more extended chase.

### **SUMMARY**

1. *P. oscillans*, as indicated by the few cranial and dental structures preserved and discovered to date, is clearly a long faced animal with a well-developed capacity to grasp, pierce and hold items to be ingested that are themselves liable to dislocate the grasper.
2. The items ingested contain both structurally resistant material through which cracks may be propagated by puncture-crushing as well as soft and tough material that may be processed by all of shearing, milling, and crushing. The material contained a quantity of irregular fragments harder than enamel capable of making abrasion grooves on surfaces of teeth, such as those usually attributed in carnivores to grit inclusions in the fur of prey; however, the distribution of shearing surfaces continuously along the molar row indicates that the material ingested was also fibrous requiring shearing – not only crushing.
3. The molar structure is not that required for shearing materials with fibre bundles such as those of grasses and leaves with characteristics outlined by Sanson (1989). Moreover, in the micro-grooving present in the enamel, there is no indication of the uniform features produced by opaline phytoliths characteristic of the teeth of grazers (Walker et al. 1978).
4. The most extensive puncture crushing, apart from incidental damage at sharp cusps, is concentrated in a relatively few areas of the premolars and along the molar rows. Indicating that brittle resistant parts of the items ingested could be located deliberately at particular points within the tooth row as is done by Canidae.
5. The condylar position relative to the tooth row and the cylindrical form of the condyle are typical of carnivorous mammals and not of herbivores or omnivores.
6. The view that *P. oscillans* is necessarily less carnivorous and more herbivorous than

other Propleopinae with larger premolars and reduced molars is not supported. Instead, if *P. oscillans* is a carnivore, as the evidence presented here suggests, it can equally well be interpreted as indicating the existence of a branch of long-faced carnivores among diprotodont marsupials with wide gape and with shearing distributed along an unreduced molar row comparable with the Thylacinidae, but having the additional capability of premolar shear.

7. The partial humerus described by Pledge (1981) and a second less complete one described here are attributed to *P. oscillans* on the dual basis that they cannot be attributed to any other taxa known from Henschke's Fossil Cave and that they are very similar in a great many respects to the equivalent bone in *H. moschatus*.

8. The humeri attributed to *P. oscillans* share features with those of *H. moschatus* which set both forms apart from bipedal macropodiform marsupials and suggest that the fossil form was consistently quadrupedal during normal terrestrial locomotion.

9. Although the humeri attributed to *P. oscillans* exhibit some similarity in form to those of certain atypical arboreal mammals (upright postured primates and sloths), certain features of morphology argue against the fossil having been arboreal.

10. Similarities of form between the humeri of *P. oscillans* and those of cursors suggest that the former may have been a capable runner. However, these similarities, and the development of muscles indicated by them, are suggestive of moderate speed endurance running rather than high speed sprinting capabilities.

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## ENDNOTES

<sup>1</sup> Specimen numbers which do not include an institutional name refer to the collection of the South Australian Museum. Material from other collections is abbreviated as follows: ANU DBZ = Australian National University, Division of Botany and Zoology; ANU PL = Australian National University, Palaeontology Laboratory (Dept. Geology); ANWC = Australian National Wildlife Collection (Division of Wildlife and Ecology, CSIRO); NMA IAC = National Museum of Australia, Institute of Anatomy Collection; NMV = Museum of Victoria; Qd Mus. = Queensland Museum; UWZS = University of Wisconsin Zoological Museum.

<sup>2</sup> At this stage of knowledge of dental development, it is a matter of preference as to whether the small tooth found in some species immediately after the large lower incisor is designated a canine or an incisor. Currently it seems probable that the large procumbent incisor of macropodiforms is not  $I_1$ . But the evidence which suggests that it is  $I_3$  or  $I_4$  requires re-evaluation (see Ride 1962, Luckett 1993). If it is  $I_4$  it is the last of the incisor series and the small tooth following cannot be an incisor. Here, following Flower (1868), we call the small tooth a canine and, following custom, continue to designate the procumbent tooth  $I_1$ .

<sup>3</sup> This is the designation used on South Australian Museum labels, but we use the shortened locality name Henschke's Fossil Cave throughout this work except where information is taken directly from such labels.

<sup>4</sup> The palatal fissure (associated with Jacobson's Organ) and the anterior palatal foramen (which transmits a branch of the Vth cranial nerve) have a common opening in *Propithecus*. Because the two are separate in some mammals (e.g. in *Aepyprymnus*), following Hildebrand (1988, fig. 8.21) the term palatal fissure is preferred, it being the larger of the two confluent components. Besides which, the term 'fissure' avoids confusion with the different anterior palatine foramen in the horizontal plate of the palatine bone.

<sup>5</sup> The terms attrition and abrasion are used here to describe wear features as follows: attrition is fine polished wear, usually planar and presumably the result of tooth-on-tooth contact, although soft and tough material between closely opposed surfaces will produce a similar effect; abrasion is irregular wear not resulting in planar features, it consists of pits, gouges and grooves (and even fine polish) and is presumably the result of ingested materials containing abrasive items such as grit, bone fragments, phytoliths, or by the polishing action of soft materials, being forced along or across the tooth surface during the power stroke of mastication. Abrasion features overlie planar attrition facets.

<sup>6</sup> Ride (1962, p. 302 footnote) has argued that the widespread occurrence of a character within a related group of organisms can be used to determine the antiquity of the character within the group.

<sup>7</sup> Thegosis or tooth sharpening is a process by which mammals use tooth-on-tooth attrition to maintain sharpness or edges (including angle of contact). There is debate about the mechanics of the process and its extent, but there is no doubt that it occurs in some mammal teeth such as the lower incisors of rodents and the canines of baboons (Kay and Hiiemae 1974 p. 254). In *P. oscillans* the occurrence of incisor wear facets in newly erupted teeth close behind the enamel tipped crowns seems to justify the conclusion that incisor thegosis occurred in this species and that it probably commenced in the pouch.

<sup>8</sup> Sanson 1989, pp. 154-57, in a most valuable review of his own and other studies clarifying relationships between principles of tooth design, function and food materials with respect to different forms of herbivory, redefines the terms cutting, shearing, crushing, and grinding. In addition, he distinguishes between the different processes high amplitude shearing and fine shearing (distinguishing the latter from grinding). His definitions and terminology are adopted here with the addition of the terms puncture crushing (see Hiiemae and Crompton 1985, p. 281) to describe the process whereby crack propagation in hard brittle food takes place from a blunt cusp or edge without shearing blades being brought into play, and point shearing and point crushing to describe occurrences of high amplitude shearing and puncture crushing at a particular place in the tooth row.

<sup>9</sup> The separate names given to the components of the adductor muscle mass are used here to simplify description and do not imply that these are discrete muscles. In *Didelphis* and *Macropus* the divisions between the elements are not clear (Hiiemae and Crompton 1985; Ride 1959) but different components of the mass function in a coordinated manner. Hiiemae and Jenkins (1969, pp. 4-6) discuss the anatomy of the mass and alternative terminologies for its components.

<sup>10</sup> It should be noted that in both of these species, in the last upper molar the posterior, non-occluding, moiety is reduced. In the lower tooth rows, the complete last lower molar is retained (and enlarged). In *Thylacinus* the crushing elements are reduced – it is said to be a specialized soft-parts feeder (like the cheetah) while in *Sarcophilus*, that eats both flesh and bone (apparently without discriminating), the crushing elements are exaggerated, as well as shearing elements being maintained.

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